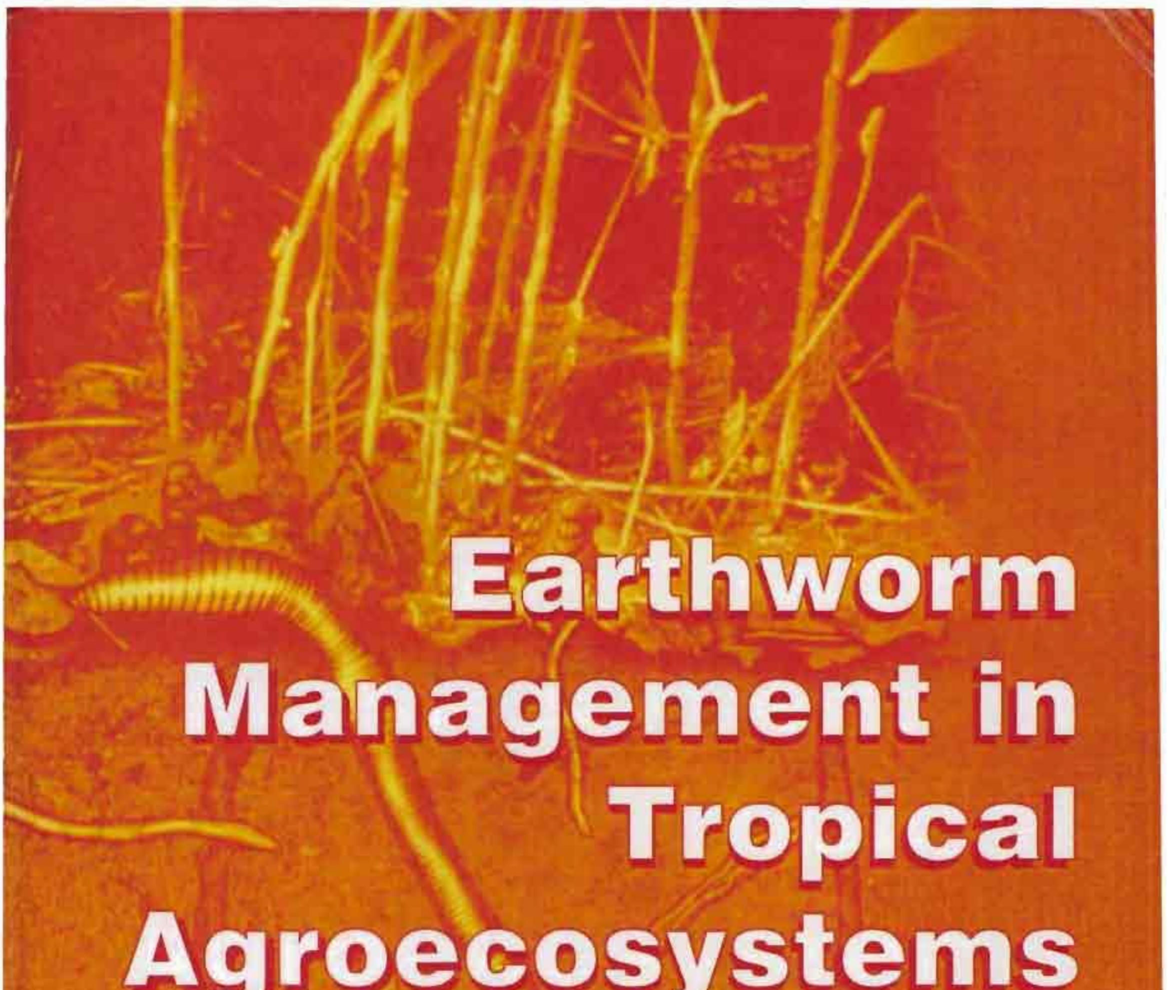

Earthworm Management in Tropical Agroecosystems

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

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EARTHWORM MANAGEMENT IN TROPICAL AGROECOSYSTEMS

Earthworm Management in Tropical Agroecosystems

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CABI Publishing	CABI Publishing
CAB International	10E 40th Street
Wallingford	Suite 3203
Oxon OX10 8DE	New York, NY 10016
UK	USA
Tel: +44 (0)1491 832111	Tel: +1 212 481 7018
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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

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Acknowledgements

This book synthesizes research done by the MACROFAUNA network from 1989 to 1996 as part of the activities of the Tropical Soil Biology and Fertility Programme. The TSBF programme provided inspiration and scientific support to the project and its contribution was greatly appreciated. The CCE-STD programme gave most of the financial resources and considerable administrative support. We thank Mario Catizzone who was our correspondent at the CCE and always gave us good advice, help and support, and Tim Hall who was the head of the Science and Technique for Development programme.

Foreword

Earthworms appeared on Earth 600 million years ago. They have since accompanied the build up and evolution of most soils and participated in the conservation of natural fertility; in a number of places they are part of all local mythologies and often pharmacopoeia. They have been called the 'intestine of the earth' by Aristotle 22 centuries ago and praised by Darwin (1884) as powerful actors in 'the formation of vegetable mould', whereas others related their abundance to the emergence of the greatest civilizations on earth. Although the latter hypothesis could hardly be tested, there is no doubt that they are important contributors to life in soil and their contribution to soil fertility has been strongly emphasized by all the scientists that would look at them and evaluate the consequences of their activities.

In spite of the convictions of Darwin and other less well known early ecologists, theoreticians and practicians in the green agricultural revolution paid no attention at all to earthworms. Their participation in soil and ecosystem function, however, was progressively being documented, mainly in soils from temperate countries, and soil ecologists have become increasingly convinced that they might be the missing link, a resource that should be used to provide such 'ecosystem services' as the conservation and gestion of soil organic matter and nutrients, and maintenance of favourable soil physical properties for plants.

Based on 20 years of preliminary research on the basic biology and ecology of earthworms in the humid tropics, the Macrofauna network has been organized to specifically address this question, within the Tropical Soil

Biology and Fertility Programme (TSBF, MAB-UNESCO). From 1990 to 1996 two collaborative projects funded by the European Community (STD2 and 3, DGXII) have been run successively by *c.* 40 scientists and students in 12 different tropical countries with participation of institutions from three European and four tropical countries, coordinated overall by IRD.

Eight complementary programmes have been developed that study earthworms as a resource, ranging from extensive inventories and organization of databases to the design of innovative technologies and deposition of a patent, i.e.:

1. A database of *c.*500 species found in tropical regions, with special emphasis on those that can adapt soil conditions in agroecosystems;
2. A comprehensive study of over 200 soil macroinvertebrate and earthworm communities, aiming to clarify the mechanism of their structure and relationships with other soil invertebrates;
3. A detailed assessment of demographic and autoecological characteristics of 26 species chosen for their occurrence in agroecosystems;
4. A quantification of the effect of earthworms (13 species tested) on plant growth (14 species involved);
5. Assessment of the effects of earthworm activities on dynamics of soil organic matter and,
6. Soil physical properties;
7. Development of 'in soil' technologies based on the stimulation and orientation of earthworm activities;
8. The analysis at a few sites of the perception and use of earthworms in tropical farming systems.

A further chapter has been added to present vermicomposting technologies.

Jaak Sinnaeve
CCE, DG XII

A Survey of Tropical Earthworms: Taxonomy, Biogeography and Environmental Plasticity

1

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Summary

A worldwide survey of earthworms in the humid tropics revealed that 51 exotics and 151 native species are commonly found in tropical agroecosystems. On the basis of frequency records and climatic and edaphic ranges, 21 exotics and 27 native species have been selected as possible candidates for manipulation. A multivariate analysis separated these species into four groups: (i) native species with wide edaphic and medium climatic tolerances; (ii) exotic species with wide climatic and edaphic tolerances; (iii) native and exotic species with narrow edaphic tolerances but more resistant to climatic variations; and (iv) native species with limited tolerance for climatic and edaphic variations.

Regarding management, species of group (ii) seem to be the most adaptable, both at regional and local levels (multipurpose species); group (i) can be managed for specific climatic conditions whereas group (iii) should be managed in specific soil environments. Species of group (iv) may only be managed at a very local scale.

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Introduction

Earthworms are confined to the soil and, for the majority of tropical farmers and agronomists, their diversity, activities and effects on soils are totally unknown. Even in the field of tropical soil science, the situation is not very different. For example, just a few years ago, there was little concern about earthworm diversity and the possible role of this diversity in the fertility of agroecosystems. During the last 10 years, however, there has been an increasing interest in diversity mainly due to the biodiversity crisis, which could be defined as the dramatic loss of species, habitats and ecological interactions (Wilson, 1985; Wilson and Peter, 1988; McNelly *et al.*, 1990). Although the most diverse tropical biota are insects that spend part of their life cycles in the soil, this environment has been, from a biodiversity viewpoint, one of the least studied.

Earthworms are not very diverse, and our current estimations of the number of existing species are far from complete. The most recent account of earthworm diversity (Reynolds, 1994) comprises 3627 earthworm species described worldwide, with an average annual addition of 68 species. The overall richness is expected to be at least twice this value, with the majority of still unknown species living in the tropics. For most species, the original description is the only information available, and nothing is known about their distribution, ecology, demography, physiology and resistance to disturbance. For example, on the basis of the number of native species found in two moderately well sampled regions, the state of Veracruz, Mexico, 33 species (Fragoso, in press), and Puerto Rico, 18 species (Borges, 1988; Borges and Moreno, 1989, 1990a,b, 1991, 1992), it is possible to predict the possible number of native species to be found in six scarcely sampled countries: three Central American continental countries (Honduras, Nicaragua and Guatemala) and three larger Caribbean islands (Cuba, Hispaniola and Jamaica). In the first group, nearly 50 species per country should be found in the future, whereas in the second group the number of species expected to be discovered is approximately ten (Jamaica), 130 (Hispaniola) and 200 (Cuba). This means that if sampling in these two regions is made with an effort similar to that in Veracruz and Puerto Rico, we should expect to find nearly 500 new native species in the future. Similar conclusions have been reached for Tasmania and Australia, where 150 and 600 species, respectively, are expected to be found once inventories are completed (Kingston and Dyne, 1995).

This chapter is the result of a 6-year project focused on characterizing the identity of earthworms in natural and managed ecosystems of the tropics (outlined in Fragoso *et al.*, 1995). The main objective was to select a group of earthworm species with potential for management in tropical agroecosystems, according to the following criteria: (i) a wide distribution; (ii) with adaptations to a wide range of environmental and edaphic conditions; and (iii) resistance to disturbances induced by agriculture.

Storage and Analysis of Data

The survey was conducted in selected regions of the tropics, and included field sampling and literature data. Most field data were obtained from the experimental sites related to this project (the MACROFAUNA network, see Chapters 4 and 5). Although it was not the principal objective, this survey allowed the discovery and description of approximately 50 new species.

EWDBASE: a database of tropical earthworms

All the information was stored in a database (EWDBASE) that includes information on the taxonomy and distribution of earthworm species, earthworm and other macroinvertebrate communities, climate of localities, edaphic and land-use variables, and socioeconomic aspects of agricultural lands where available.

Inputs to EWDBASE (climatic, edaphic and species distribution data) were taken from the following published literature: Mexico, Central America and the Caribbean islands (Eisen, 1895, 1896, 1900; Michaelsen, 1900, 1908, 1911, 1912, 1923, 1935, 1936; Cognetti, 1904a,b, 1905, 1906, 1907, 1908; Pickford, 1938; Gates, 1954, 1962a,b, 1970a,b, 1971, 1972, 1973, 1977a,b, 1979, 1982; Graff, 1957; Righi, 1972; Righi and Fraile, 1987; Sims, 1987; Borges, 1988, 1994; Borges and Moreno, 1989, 1990a,b, 1991, 1992; Fraile, 1989; James, 1990, 1991, 1993; Csuzdi and Zicsi, 1991; Zicsi and Csuzdi, 1991; Fragoso, 1993, in press; Rodríguez, 1993; Fragoso and Rojas, 1994; Reynolds and Guerra, 1994; Reynolds and Righi, 1994; Fragoso *et al.*, 1995; Reynolds *et al.*, 1995; Rodríguez and Fragoso, 1995), Bolivia (Rombke and Hanagarth, 1994), Ivory Coast (Omodeo, 1958; Lavelle, 1978, 1983; Tondoh, 1994), Congo (Zicsi and Csuzdi, 1986), Ghana (Sims, 1965), Gambia (Sims, 1967), Peru (Yurimaguas; Lavelle and Pashanasi, 1988) and several regions from India (Senapati, 1980; Chaudry and Mitra, 1983; Julka, 1986, 1988; Julka and Paliwal, 1986; Julka and Senapati, 1987; Bhadauria and Ramakrishnan, 1989; Julka *et al.*, 1989; Bano and Kale, 1991; Blanchart and Julka, 1997). EWDBASE was also fed with data obtained from field sampling carried out in Mexico, Panama, Colombia, Ivory Coast, India, Martinique, Guadaloupe, Rwanda, Peru, Congo and Cuba by members of the macrofauna network.

EWDBASE included data relating to 457 species, 745 localities and 836 sites from 28 countries. Distribution and environmental plasticity were analysed by relating species distribution to climate (1310 records), soils (818 records) and types of land use (1755 records).

Data analysis

Data were analysed at three geographic levels, i.e. local, regional and worldwide. At the local level, we intended to characterize the persistence of native earthworm species in different land-use systems (e.g. conversion of tropical deciduous forests to maize or pastures in Panuco, Mexico; maize plantations in native savannas of Lamto, Ivory Coast or the eastern llanos of Colombia; tea plantations in cloud forests of India, etc.). At the regional level, the analysis was extended to geographic areas such as southern Mexico, northern Rwanda or the Baoule region around Lamto (Ivory Coast), with the aim of identifying widespread native species. The worldwide analysis evaluated the distribution of exotic species in different natural and managed tropical ecosystems. The integration of these data in a global analysis produced three main outputs: (i) a list of tropical species of worldwide distribution that can be manipulated in any agroecosystem; (ii) regional lists of species by countries and/or kinds of agroecosystems; and (iii) an evaluation of the environmental and edaphic plasticity of these selected species.

Earthworm species of EWDBASE were classified along three different axes:

1. Biogeography, to divide species depending on this origin into natives and exotics. Native earthworms are those species that evolved in the site or region under study. Exotic species are earthworms that did not originate in the site under study and that were, generally, introduced by human activities; these species have also been called peregrine (Lee, 1987) and anthropochorous (Gates, 1970c).
2. Distribution among land-use systems, to separate species on the basis of their capabilities to adapt to natural (e.g. primary forests or savannas) or managed (e.g. annual crops or pastures) systems.
3. Ecological plasticity, to rank earthworms according to their ecological tolerance to edaphic and environmental variables from stenoecic (narrow range) to euryoecic (wide range) species.

These three axes were combined with the three geographic scales of analysis (local, regional and global) in order to propose the most appropiate earthworm species for manipulation in a given region and/or country in a specific agricultural situation.

Earthworm Species of Tropical Agroecosystems

The exotic earthworms of the tropics

Since the early studies of Eisen (1900) and Michaelsen (1903, 1935), it has been observed that peregrine worms were very common in tropical disturbed ecosystems. In a paper that analysed the distribution and dispersal of this group of species, Lee (1987) stated that these species '... more than any others, . . . are important in maintaining soil fertility in agricultural and pastoral lands.' Although the author did not present the complete list of species, he mentioned that peregrine species comprise nearly 100 species (approx. 3% of all earthworms). Peregrine earthworms become exotics when the geographic area of occurrence does not correspond to the original area of distribution.

The number of records of tropical exotic species is enormous, and their distribution should be analysed using the three scales mentioned above (worldwide, regional and local), because some species with wide distributions may be restricted to one kind of land-use system or have narrow climatic and edaphic niches that are not represented in a given country or continent.

From EWDBASE and a literature review (Gates, 1972, 1982; Lee, 1987; Mele *et al.*, 1995), we identified 51 exotic species commonly distributed across tropical countries (Table 1.1). Fifteen were temperate Lumbricidae of European origin, restricted to high altitude mountain localities. Their frequent occurrence in natural temperate forests suggests that these species may have replaced natives, as has been observed by Fragoso (in press) in the temperate forests of Veracruz, Mexico. The absence of this group of exotics in low altitude tropical agroecosystems (from EWDBASE queries) eliminates their potential for manipulation and, therefore, this group of species will no longer be considered in this chapter.

From Table 1.1, we selected a group of 20 species distributed worldwide, which are mainly from localities below 1000 m. This group is presented in Table 1.2, ranked according to their frequencies in agroecosystems; Table 1.3 shows, for the above group of species, the ranges of environmental (precipitation and temperature) and edaphic (pH, organic matter, nitrogen, sand and clay) situations in which they occur. From the data in Tables 1.2 and 1.3, it is possible to make a preliminary separation of another group of species adapted to different managed agroecosystems and with wide ranges of environmental and/or edaphic plasticity. These species include *Pontoscolex corethrurus, Polypheretima elongata, Dichogaster bolaui, Ocnerodrilus occidentalis, Amynthas gracilis, A. corticis, Dichogaster affinis* and *D. saliens*, and all of them are tolerant to very low soil concentrations of nutrients, organic matter and nitrogen.

The widespread native earthworms of the tropics

The majority of native species are not very tolerant and are restricted mainly to natural environments. Of the 404 native species stored in EWDBASE, 274 species (67%) were restricted to a single locality, whereas 207 (51%) were found exclusively in natural environments. On the other hand, nearly 40% of native species of EWDBASE were found inhabiting at least one of five types of agricultural land-use systems: pastures, crops, tree plantations, organic wastes and fallows (Table 1.4). Only a small proportion of these native species,

Continued p.16

Table 1.1. The exotic earthworms of the tropics. Continental, country and altitudinal distribution.

Species	Family	Origin	Distribution Continents	 Countries	Altitude (m) (average)
Allolobophora chlorotica	Lumbricidae	Europe	3	34	3000
Amynthas corticis	Megascolecidae	Asia	5	40	0–2500 (1243)
Amynthas gracilis	Megascolecidae	Asia	5	31	0–2000 (962)
Amynthas morrisi	Megascolecidae	Asia	4	23	610
Amynthas rodericensis	Megascolecidae	Asia	3	26	0–1200 (420)
Aporrectodea caliginosa	Lumbricidae	Europe	4	15	1150–3850 (3168)
Aporrectodea longa	Lumbricidae	Europe	5	27	2240–2400
Aporrectodea rosea	Lumbricidae	Europe	5	52	500–4650 (2972)
Aporrectodea trapezoides	Lumbricidae	Europe	5	19	1200–3300 (2650)
Aporrectodea turgida	Lumbricidae	Europe	5	20	1300–3400 (2570)
Bimastos parvus	Lumbricidae	N. America	5	32	12–1500 (756)
Bimastos tumidus	Lumbricidae	N. America	1	1	1000–1270 (1135)
Dendrobaena octaedra	Lumbricidae	Europe	4	32	1200–4650 (2423)
Dendrodrilus rubidus	Lumbricidae	Europe	5	46	950–4650 (2442)
Diachaeta thomasi	Glossoscolecidae	S. America	1	2	Sea level
Dichogaster affinis	Dichogastrini*	W. Africa	4	24	0–1400 (391)
Dichogaster annae	Dichogastrini*	W. Africa	2	5	60–1940 (1438)
Dichogaster bolaui	Dichogastrini*	W. Africa	5	43	0–1360 (259)
Dichogaster gracilis	Dichogastrini*	W. Africa	2	2	Under 500
Dichogaster modigliani	Dichogastrini*	W. Africa	4	20	0–1100 (339)
Dichogaster saliens	Dichogastrini*	W. Africa	4	17	0–1100 (307)
Drawida barwelli	Moniligastridae	India	2	11	0–1000 (347)
Eisenia fetida	Lumbricidae	Europe	5	45	1300–1500 (1394)
Eiseniella tetraedra	Lumbricidae	Europe	5	45	1300–3820 (3109)

Eudrilus eugeniae	Eudrilidae	W. Africa	4	31	0–60 (15)
Eukerria kukenthali	Ocnerodrilidae	S. America	2	8	n.d
Eukerria mcdonaldi	Ocnerodrilidae	S America	1	1	300
Eukerria peguana	Ocnerodrilidae	S. America	1	1	n.d.
Eukerria saltensis	Ocnerodrilidae	S. America	4	10	550–3875 (1911)
Eukerria zonalis	Ocnerodrilidae	S. America	1	1	300
Gordiodrilus peguanus	Ocnerodrilidae	C. Africa	4	7	n.d.
Hyperiodrilus africanus	Eudrilidae	W. Africa	1	6	n.d.
Lumbricus rubellus	Lumbricidae	Europe	5	34	1500–3750 (2739)
Lumbricus castaneus	Lumbricidae	Europe	3	23	n.d.
Lumbricus terrestris	Lumbricidae	Europe	5	36	n.d.
Metapheretima taprobanae	Megascolecidae	Asia	4	7	10–40 (30)
Metaphire californica	Megascolecidae	Asia	5	21	0–2000 (982)
Metaphire houlleti	Megascolecidae	Asia	5	20	10–853 (408)
Metaphire posthuma	Megascolecidae	Asia	2	12	12–22 (17)
Microscolex dubius	Acanthodrilinae*	S. America	5	16	n.d.
Microscolex phosphoreus	Acanthodrilinae*	S. America	5	28	1500–3600 (1506)
Nematogenia panamaensis	Ocnerodrilidae	C. America	3	12	n.d.
Ocnerodrilus occidentalis	Ocnerodrilidae	C. America	5	22	0–1520 (470)
Octolasion cyaneum	Lumbricidae	Europe	5	30	1050–2430 (1576)
Octolasion tyrtaeum	Lumbricidae	Europe	5	35	1180–4654 (2313)
Periscolex brachycystis	Glossoscolecidae	C. America	1	4	0–500 (192)
Peryonix excavatus	Megascolecidae	Asia	4	19	300–1050 (1077)
Pheretima bicincta	Megascolecidae	Asia	3	12	30–1100 (577)
Polypheretima elongata	Megascolecidae	Asia	4	27	0–1300 (185)
Polypheretima taprobanae	Megascolecidae	Asia	4	7	1360
Pontoscolex corethrurus	Glossoscolecidae	S. America	4	56	0–2000 (463)

*Tribe or subfamily of Megascolecidae; n.d. = not determined.

Table 1.2. Distribution of common exotic earthworms in different tropical land-use systems. No. of records from Mexico, Central America, the Caribbean, Colombia, Rwanda, Congo, Ivory Coast and India.

Species	Natural ecosystems	Crops	Pastures	Tree plantations	Fallows	Organic wastes
Pontoscolex corethrurus	94	31	44	41	6	4
Polypheretima elongata	30	10	39	19	4	5
Dichogaster bolaui	11	7	15	11	3	5
Ocnerodrilus occidentalis	3	6	15	7	2	1
Amynthas gracilis	7	4	6	9	2	2
Amynthas corticis	22	6	7	4	2	2
Hyperiodrilus africanus	2	4	8	5	1	2
Dichogaster affinis	9	5	5	7	1	0
Dichogaster saliens	5	1	9	4	1	0
Drawida barwelli	3	1	9	3	0	0
Eudrilus eugeniae	2	0	3	3	0	4
Dichogaster annae	0	2	2	4	0	1
Amynthas rodericensis	24	1	5	3	0	0
Peryonix excavatus	1	0	1	1	0	5
Metaphire californica	0	0	4	0	0	1
Dichogaster modigliani	1	0	4	1	0	0
Metaphire houlleti	0	0	4	0	0	0
Metapheretima taprobanae	2	0	2	1	0	0
Periscolex brachycystis	6	1	2	1	0	0
Pheretima bicincta	5	0	0	1	0	0
Metaphire posthuma	1	0	0	1	0	0

Table 1.3. Range of environmental conditions tolerated by the most common exotic species.

Species	T (°C)	Rainfall (mm)	pH	OM (%)	N (%(× 0.1))	Ca (mEq 100 g^{-1})	Mg (mEq 100 g^{-1})	S (%)	C (%)
Pontoscolex corethrurus	14–28	268–5000	3.8–8.2	0.9–12.6	0.1–9	0.8–16.5	0.1–11.2	3–91	6–87
Polypheretima elongata	21–30	800–4000	5–7.8	1.8–7.6	0.8–3.8	4.4–53	1–2.7	5–93	4–54
Dichogaster bolaui	18–30	800–4725	5–8.2	1–10.2	0.2–8.8	1.7–44	0.06–9	5–93	4–53
Ocnerodrilus occidentalis	16–30	146–4725	5.6–8.9	0.9–7.8	0.7–8.9	0.8–53	0.06–4.5	18–98	2–74
Amynthas gracilis	15–26	670–3500	4.8–8.9	1.7–14.4	0.7–5.9	1.3–3.4	0.7–.46	11–61	9–53
Amynthas corticis	13–26	865–4521	3.9–7.5	2–12.6	2–4.2	1.9–5.8	1.5–3.5	36–61	17–33
Dichogaster affinis	17–28	440–2240	4.5–8.2	1–13.7	0.7–8.8	0.82–53	0.06–4.9	9–98	2–74
Dichogaster saliens	22–28	916–4725	5–8.9	0.6–6.2	0.2–8.9	0.9–12.5	0.06–4.5	18–91	6–47
Drawida barwelli	21–26	1500–4000	5–7.9	3.6–5.4	2–2.5	3.5–5.8	1.1–3.5	3–42	24–87
Eudrilus eugeniae	25–28	1352–1880	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Dichogaster annae	28	1880	3.7–6.3	1.6–4.9	1–2.6	n.d.	n.d.	32–85	11–54
Amynthas rodericensis	20–26	1200–5000	4.7–8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Peryonix excavatus	15–24	865–2173	7.1–7.5	3	n.d.	n.d.	n.d.	50	33
Metaphire californica	21	2631	5.2–5.6	4.3–5.4	2.2–2.5	3.5–5.8	1.5–3.5	36–42	24–28
Metaphire houlleti	22–26	1314–1996	6.8	2	n.d.	n.d.	n.d.	n.d.	n.d.
Metapheretima taprobanae	26	1450–2000	6.4–8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Dichogaster modigliani	25	1396	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Periscolex brachycystis	24–28	1880–4725	5–6.5	2.2–7.6	1.1–4.2	4.1–44	1.1–3.6	5–62	9–50
Pheretima bicincta	21–26	2500–3500	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Metaphire posthuma	24	916–1079	8.1	1.2	1	6.6	0.86	46	18

T = temperature, OM = organic matter, N = nitrogen, Ca = calcium, Mg = magnesium, S = sand, C = clay; all values from the upper 10 cm of soil.

Table 1.4. Native earthworm species of tropical agroecosystems.

Species	C	P	T	F	W
Belize					
Diplotrema jenniferae		1			
Bolivia					
Andiorrhinus bolivianus	1				
Enantiodrilus borelli		1			
Eukerria asuncionis	1				
Eukerria eiseniana		1			
Eukerria garmani		1			
Eukerria tuberculatus			1		
Goiascolex vanzolinii			1		
Colombia					
Andiodrilus yoparensis	1	1			
Andiorrhinus sp.nov1		1			
Glossodrilus sikuani	1	1			
***Glossodrilus* sp1**	**1**	**2**	**2**	**3**	
Martiodrilus agricola	1			2	
Martiodrilus carimaguensis	1	1			
Martiodrilus savanicola	1			1	
Martiodrilus sp1	1			3	
Thamnodrilus sp1				2	
Congo					
Dichogaster graffi			1		
Gordiodrilus sp1			1		
Nematogenia lacuum			1		
Costa Rica					
Glossodrilus dorasque			1		
Glossodrilus nemoralis		4			
Glossodrilus orosi		1			
Cuba					
Diplotrema ulrici	1				
Onychochaeta elegans	**1**	**4**	**4**		
Onychochaeta windlei	**2**	**2**	**3**		
Pontoscolex cynthiae	1		3		
Zapatadrilus morenoae	1	1			
Zapatadrilus siboney			1		
Zapatadrilus taina			1		
El Salvador					
Eutrigaster sporadonephra			1		
Guadaloupe					
Pontoscolex spiralis	1	2	1		

Table 1.4. *Continued.*

Species	C	P	T	F	W
India					
Curgiona narayani	3				
Drawida ampullacea	**1**	**3**	**1**	**2**	
Drawida assamensis				1	
Drawida calebi	**1**	**1**	**2**		
Drawida fakira	1				
Drawida ferina	2		1		
Drawida ghatensis			1		
Drawida japonica	1	1	1		
Drawida kanarensis	1		1		
Drawida lennora	1			1	
Drawida modesta	1			1	
Drawida nepalensis	**1**	**2**			
Drawida paradoxa	**1**	**10**	**1**	**1**	
Drawida pellucida	2		1	1	
Drawida sp1	1				
Drawida sp2		1			
Drawida scandens		1	1		
Drawida sp3		4	1		
Drawida sulcata	1		1	1	
Drawida thurstoni		4		1	
Drawida willsi	**1**	**3**	**1**		
Eutyphoeus festivus				2	
Eutyphoeus incommodus	**2**	**3**			
Eutyphoeus orientalis		1			
Eutyphoeus sp1	1				
Eutyphoeus waltoni	1				
Gen.nov1 sp.nov1		**8**	**1**		
Gen.nov1 sp.nov2		2			
Gen.nov2 sp.nov1		1		1	
Gen.nov3 sp.nov1		3			
Glyphidrilus tuberosus		2			
Glyphidrilus annandalei	1			2	
Hoplochaetella kempi	1		1	1	
H. sanvordemensis		1			
Hoplochaetella suctoria			1		
Hoplochaetella sp1		1			
Hoplochaetella sp2		2			
Karmiella karnatakensis		**6**	**1**		
Karmiella sp1		1			
***Konkadrilus* sp1**		**6**	**1**	**1**	
Konkadrilus sp2		8	2		
Konkadrilus tirthahalliensis			6		
Lampito mauritii	**3**	**2**	**5**	**1**	
Lennogaster chittagongensis		1			

Continued

Table 1.4. *Continued.*

Species	C	P	T	F	W
Lennogaster pusillus	**3**	**3**			
Lennogaster sp1			1		
Lennoscolex sp1			1		
Lennogaster dashi			2		
Mallehulla indica		1	1	1	
Megascolex felicisetae	1				
Megascolex sp1	3				
Megascolex insignis	1		1	1	
Megascolex konkanensis		**2**	**2**	**3**	
Megascolex lawsoni	1		2		
Nelloscolex strigosus				1	
Notoscolex sp1	1				
Octochaetona beatrix	1	1	1		
Octochaetona rosea	1		1	1	
Octochaetona surensis		1	1		
Pellogaster bengalensis	1		1		
Perionyx sp1		1			
Plutellus tumidus	1		1		
Ramiella bishambari	1				
Tonoscolex horaii				2	
Travoscolides duodecimalis	1				
Wahoscolex sp1		4			
Ivory Coast					
Agastrodrilus opisthogynus			1		
Chuniodrilus palustris	**10**	**1**	**1**	**3**	
Chuniodrilus zielae	**10**	**1**	**1**	**3**	
Dichogaster agilis	**9**	**1**	**2**	**2**	
Millsonia anomala	**9**	**1**	**1**	**3**	
Millsonia lamtoiana	1		1	1	
Millsonia schlegeli		2			
Jamaica					
Eutrigaster grandis	1				
Martinique					
Pontoscolex cuasi		1			
Pontoscolex spiralis	**1**	**2**	**2**		
Mexico					
Balanteodrilus pearsei	**4**	**10**	**1**	**2**	**2**
Diplocardia eiseni		1			
Diplocardia sp.nov1		6			
Diplocardia sp.	1				
Diplocardia sp.nov2	3		6	1	
Diplotrema sp.nov1		1			
Diplotrema murchiei	**1**	**11**		**3**	

Table 1.4. *Continued.*

Species	C	P	T	F	W
Diplotrema papillata		4			
Gen.nov4 sp.nov1		3			
Gen.nov5 sp.nov1		1			
Larsonidrilus microscolecinus		2	1		
Larsonidrilus orbiculatus		3			
Lavellodrilus maya		3			1
Lavellodrilus parvus	**5**	**5**	**1**	**1**	
Lavellodrilus riparius		1			
Mayadrilus rombki	1				
Phoenicodrilus sp.nov1		1		1	
Phoenicodrilus taste	**1**	**16**	**2**		
Protozapotecia australis	**1**	**6**	**1**	**1**	
Ramiellona sp.nov1			1		
Ramiellona sp.nov2		1		1	
Ramiellona sp.nov3		1			
Ramiellona sp.nov4		1			
Ramiellona sp.nov5				1	
Ramiellona sp.nov6				1	
Ramiellona sp.nov7		1			
Ramiellona strigosa		**1**	**2**		
Ramiellona wilsoni		1			
***Zapatadrilus* sp.nov1**	**3**	**3**	**9**	**3**	
Zapotecia amecameca				1	
Zapotecia nova		**4**		**3**	
Zapotecia sp1		3		1	
Peru					
Diachaeta xepe	1	2	1	1	
Rhinodrilus lavellei	1		1		
Rhinodrilus pashanasi	**1**	**1**	**1**		
Rwanda					
Dichogaster itoliensis	2	1	1		
Dichogaster sp1	1	1	2		1
Eminoscolex lavellei	**3**	**1**	**5**		
***Gordiodrilus* sp1**	**4**	**1**	**15**		
Stuhlmannia variabilis	1		2		1

No. of records from EWDBASE. C=crops, P=pastures, T=tree plantations, F=fallows,W=organic wastes.

Table 1.5. Environmental tolerance ranges (climatic and edaphic) of selected tropical native earthworms (data from EWDBASE).

Species	T (°C)	Rainfall (mm)	pH	OM (%)	N (% (× 0.1))	Ca (mEq $100\ g^{-1}$)	Mg (mEq $100\ g^{-1}$)	S (%)	C (%)
Cuba									
O. elegans	28	1880	n.d.	7.6	n.d.	44	9	5	50
India									
D. ampullacea	22	5000	4.6–5.8	4.3–11	0.17–0.48	2.5–14	1–3.7	15–43	18–53
D. paradoxa	22	5000	4.4–5.1	3.6–9.3	0.19–0.33	2.4	0.93	23	40
D. willsii	30–31	1150–2363	5.9–6.8	0.9–2.4	0.08–0.38	n.d.	n.d.	83–95	2–7
E. incommodus	16–30	1014–1600	5.9–6.8	1–3	n.d.	n.d.	n.d.	n.d.	n.d.
D. nepalensis	16–26	1014–1600	6.7–6.8	1–2	n.d.	n.d.	n.d.	n.d.	n.d.
K. karnatakensis	22	5000	4.7–5.5	4.2–7.5	0.17–0.33	5.04	1.71	28	18–40
L. mauritii	24–31	865–2166	6–6.7	1–3.2	0.08–0.19	n.d.	n.d.	83–91	4–7
L. pusillus	16–30	1014–1700	5.9–6.8	1–5	n.d.	n.d.	n.d.	47	34
O. beatrix	16–24	865–1314	6.8–7.1	2	n.d.	n.d.	n.d.	n.d.	n.d.
K. sp1	22	5000	4.4–5.8	4.2–11	0.17–0.48	14.8	3.74	n.d.	18–53
K. sp2	22	5000	4.4–5.8	3.6–10.8	0.17–0.48	2.4–15	0.9–3.7	15–43	18–53
Mexico									
B. pearsei	24–27	916–2963	5.5–8.2	1–14.4	0.09–0.59	0.9–23	0.06–5	9–82	10–86
D. murchiei	24–27	916–2160	7.5–8.9	0.2–2.6	0.06–0.88	1.3–21	0.06–3	22–98	2–74
D. papillata	25–27	814–2130	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
L. parvus	24–27	1156–4725	5.3–8.1	0.9–10.1	0.07–0.42	4.5–17	0.65–11	19–63	13–74
P. taste	19–27	600–2963	5–8	1–14.4	0.08–0.42	4.1–23	0.06–6	9–78	9–86
P. australis	14–25	600–2522	5.3–7.9	1.4–11.8	0.07–0.42	5.6–14	1–6.1	11–63	12–73
R. strigosa	24–27	1000–2963	5–6.5	2.2–6.5	0.11–0.42	4.1–13	1.7–3.6	32–62	9–50
Z. sp.nov 1	24–25	916–1349	7.7–8.3	1.1–7.3	0.02–0.48	0.87–24	0.18–3	9–46	26–62

Ivory Coast									
C. palustris	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
C. zielae	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
D. agilis	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
M. anomala	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
Rwanda									
E. lavellei	n.d.	n.d.	3.7–7.4	1.6–4.9	0.08–0.24	n.d.	n.d.	32–60	29–54
G. sp1	n.d.	n.d.	3.5–7.8	1.4–41.2	0.06–1.4	n.d.	n.d.	2–92	10–67
S. variabilis	n.d.	n.d.	3.7–4.4	3.5–4.7	0.13–0.26	n.d.	n.d.	42–85	11–48

T = temperature, OM = organic matter, N = nitrogen, Ca = calcium, Mg = magnesium, S = sand, C = clay; all values from the upper 10 cm of soil.

however, are common in tropical agroecosystems (Table 1.4, 31 species in bold). This group includes species widely distributed at the regional level (e.g. *Onychochaeta elegans* in Cuba, *Balanteodrilus pearsei* in southeastern Mexico or *Lampito mauritii* in India) or locally abundant (*Ramiellona strigosa*, *Zapatadrilus* sp.nov1 in Mexico and *Millsonia anomala* in Ivory Coast). Table 1.5 shows the environmental (precipitation, temperature) and edaphic (pH, organic matter, nitrogen, sand and clay) tolerance ranges of some of these species, according to the country in which they occur. Species listed in this table are those for which these data were available.

Comparisons between exotic and widely distributed native earthworm species

So far, we have identified 20 exotic and 27 native species that commonly occur in tropical agroecosystems of Asia, Africa and America (Tables 1.2 and 1.5). Data from Tables 1.3 and 1.5 suggest that these species apparently have wide ranges of climatic and edaphic tolerances. Figure 1.1 shows that the degree of tolerance (i.e. the environmental plasticity) is larger in the group of exotics, both at the regional (range of annual precipitation) and local level (range of pH). In this figure, however, environmental plasticity is analysed with range values (difference between maximum and minimum) of only two variables. In order to determine whether this pattern is maintained with more variables, two multivariate analyses were performed using the climatic (two) and edaphic (seven) variables of Tables 1.3 and 1.5. The input matrix consisted of 47 rows (native and exotic species) and nine columns (environmental variables), data being standardized in both cases. The first analysis was a principal component analysis (PCA), that ordinated species along two components which together explained 76% of the total variance (C1 = 62%, C2 = 14%). C1 and C2 correlated, respectively, with edaphic and climatic ranges. The second analysis was a cluster analysis, performed using unweighted pair-groups method analysis (UPGMA) as an average-linkage clustering method. PCA and UPGMA were made respectively, with STATGRAPHIC and PATN (Belbin, 1976) software.

Figure 1.2 shows the result of these analyses that ordinated and grouped the native and exotic species listed in Tables 1.3 and 1.5, into four main groups:

1. G1 includes those native species with wide edaphic and medium climatic tolerances (high local plasticity but low regional plasticity), which correspond to the majority of native widespread Mexican species.
2. G2 are the common exotic species of the tropics that exhibit wide climatic and edaphic tolerances (high regional and local plasticity).
3. G3 includes species (natives and exotics) with narrow edaphic tolerances that are resistant to climatic variations (low local but high regional plasticity).

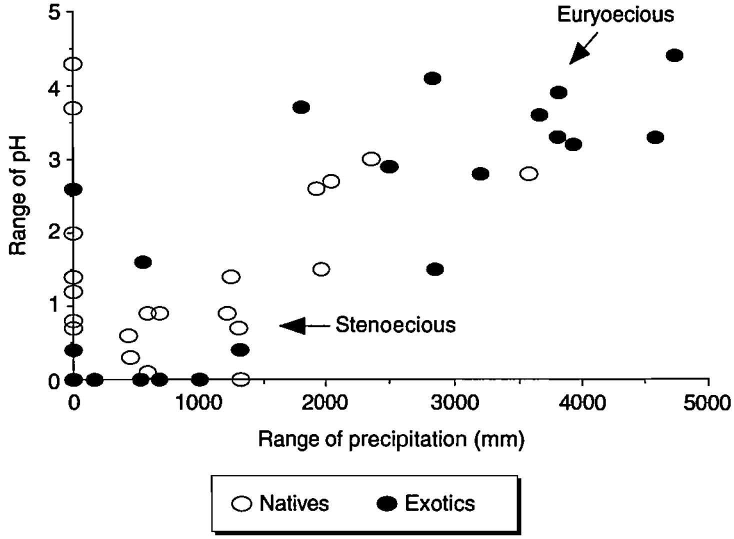

Fig. 1.1. Example of climatic (annual precipitation) and edaphic (pH) plasticity of exotic and native widespread tropical earthworm species. Each point represents a species. Those situated in the upper right corner indicate euryoecious species, whereas those situated in the lower left corner indicate stenoecious species. Both precipitation and pH are range values.

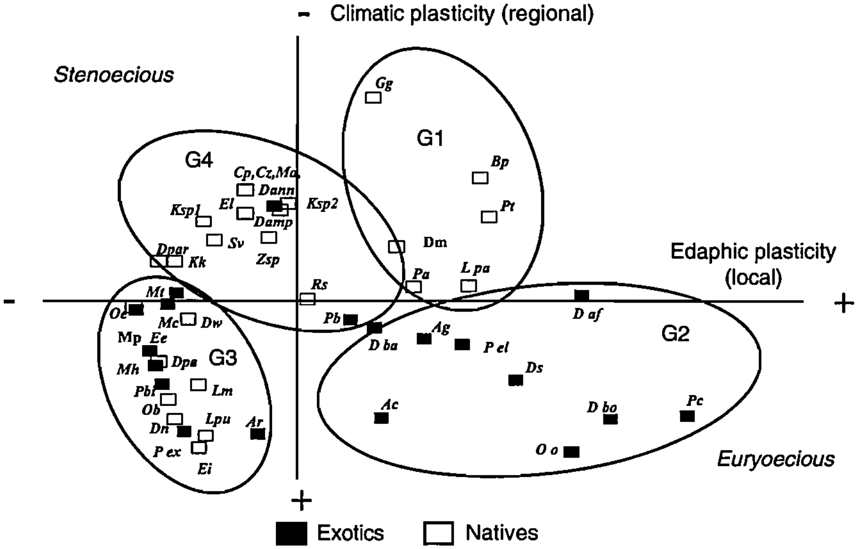

Fig. 1.2. Ordination (PCA) and clustering (UPGMA) of widespread native and exotic species on the basis of climatic and edaphic range values. For initials see Table 1.6.

4. G4 groups species with low tolerance to both climatic and edaphic variables (low regional and local plasticity). It is this group in which the majority of the other native species of Table 1.4 should be placed.

Although this analysis is somewhat biased by the amount of records and/or data available (some species have very few records and consequently low ranges), the output ordination and classification is useful because it provides a framework for the classification of earthworms with potential for manipulation, according to their ecological plasticity.

Thus, G2 (euryoecics) includes those exotic species that can be manipulated in the majority of tropical agroecosystems, both if they are introduced and if they are already present. They represent the species best adapted to unsuitable edaphic environments: *Amynthas gracilis* (*Ag*), *A. corticis* (*Ac*), *Dichogaster affinis* (*Daf*), *D. bolaui* (*Dbo*), *D. saliens* (*Ds*), *Ocnerodrilus occidentalis* (*Oo*), *Pontoscolex corethrurus* (*Pc*) and *Polypheretima elongata* (*Pe*). The last two species are endogeic mesohumic species (see Chapter 2 for a definition of these terms) which, due to their abundances, cast production and burrowing activities, have important effects on soil processes. In the same way, G1 (euryedaphic species) corresponds to native species that, for a given country and/or region, should be ranked first in manipulative practices because they represent the original adapted fauna: *Balanteodrilus pearsei* (*Bp*), *Lavellodrilus parvus* (*Lpa*), *Phoenicodrilus taste* (*Pt*), *Diplotrema murchiei* (*Dm*) and *Protozapotecia australis* (*Pa*) in Mexico and *Hyperiodrilus africanus* for several African countries (this species was not analysed for plasticity, but is very common in different land-use systems). G3 (stenoedaphic species) comprises species that could be manipulated in different regions but in the same type of soil substrate, e.g. epigeic native (*Drawida willsii, Dw*) and exotic species (*Perionyx excavatus, Pex; Eudrilus eugeniae, Ee*) on organic rich substrates. Finally, G4 (stenoecic species) represents the more local scale of management: native species that only survive in a given locality and in a given type of soil. They might be manipulated at a local level, provided no intensive or destructive practices are used (see Chapter 2). This is the case, for example, for some of the savanna species of Lamto (*Millsonia anomala, Ma*), some (but not all) forest species of Yurimaguas and several Indian (*Konkadrilus* sp1 and sp2, *Ksp1* and *Ksp2; Drawida ampullacea, Damp*) and Mexican (*Ramiellona strigosa, Rs; Zapatadrilus* sp.nov1, *Zsp*) species.

In general, this analysis shows that exotic species are better adapted than natives to factors that change both at the regional–continental level (e.g. rainfall, temperature) and at the local level (edaphic changes); the majority of natives, on the other hand, are incapable of adapting to regional variations, but some species are still able to withstand variations at a more local level.

Besides environmental plasticity, there are at least two other variables that could explain the wider distribution of exotics and the absence of native species in other regions.

1. Parthenogenetic reproduction: almost all exotic species in Table 1.2 are considered to be facultatively parthenogenetic, meaning that they may produce viable unfertilized cocoons. Native species in Table 1.4, on the other hand, only produce viable cocoons after fertilization (with a few exceptions such as *P. taste* and *O. elegans*). Parthenogenesis, therefore, appears to be an essential determinant of the wide geographic distribution of exotics, as was originally proposed by Reynolds (1974) and Lee (1987). If mating is not obligatory, one single individual (even a cocoon) may establish a new population.

2. Historical dispersal by man: the distribution of exotics has been greatly favoured by the spread of plants worldwide and such practices as the use of soil as ballast, in the days of long sea voyages. Gates (1972, 1982) intercepted, over several years, the worms that were introduced to the United States in pots containing imported plants. He found all the exotic species of Table 1.2 and many native species from several tropical and temperate countries; these species, of course, did not have any chance to establish in North American soils, but we can infer that, in the past, this situation occurred repeatedly, being the main cause for the presence of exotic species.

In some cases, it is possible to relate the distribution of some exotics to the origin of introduced plants. The African exotic species *Gordiodrilus peguanus* and *Eudrilus eugeniae*, for example, are present mainly in former European colonies (e.g. Greater Antilles; Gates, 1972) that were, in the past, dominated by an African slave population; they are not present, for example, in Mexico, Peru and other countries where this population was practically non-existent. In a number of cases, the absence of euryoecious native species in a given tropical country may, therefore, better be explained by human activities than by factors related to ecological plasticity.

Conclusions

The list of most common earthworm species of tropical agroecosystems includes a set of euryoecious exotic species, common in the majority of tropical countries, and native species that are common for a given country at local or regional levels. Table 1.6 lists these species, their ecological categories and the geographic level at which management of their populations should be considered.

Most species with potential for manipulation are large species, mainly mesohumic endogeics and epi-endogeics that live in the soil and ingest a mixture of soil and surface litter. These species can be considered as ecosystem engineers because they transform the edaphic profile through the production of casts and burrows; in this regard they are keystone species in the agroecosystem. Small polyhumic species may play a role in the system (e.g. as 'decompacting' species; see Chapter 5) but may not be crucial in the short term as their activities do not dramatically affect soil profile and other subordinated

Table 1.6. List of tropical earthworm species with potential for manipulation in annual cropping systems.

Species	Ecological category	Region	Management
Dichogaster bolaui (Dbo)	Epigeic	Humid tropics	Worldwide
Dichogaster saliens (Ds)	End. polyhumic	Humid tropics	Worldwide
Dichogaster affinis (Daf)	End. polyhumic	Humid tropics	Worldwide
Dichogaster annae (Dann)	End. polyhumic	Humid tropics	Worldwide
Drawida barwelli (Dba)	End. polyhumic	Humid tropics	Worldwide
Eudrilus eugeniae (Ee)	Epigeic	Humid tropics	Worldwide
Metapheretima taprobanae (Mt)	End. mesohumic	Humid tropics	Worldwide
Metaphire californica (Mc)	Epi–endogeic	Humid tropics	Worldwide
Metaphire houlleti (Mh)	Epi–anecic	Humid tropics	Worldwide
Metaphire posthuma (Mp)	End. mesohumic	Humid tropics	Worldwide
Ocnerodrilus occidentalis (Oo)	End. polyhumic	Humid tropics	Worldwide
Periscolex brachycystis (Pb)	End. polyhumic	Humid tropics	Worldwide
Peryonix excavatus (Pex)	Epigeic	Humid tropics	Worldwide
Pheretima bicincta (Pbi)	Epi–endogeic	Humid tropics	Worldwide
Polypheretima elongata (Pel)	End. mesohumic	Humid tropics	Worldwide
Pontoscolex corethrurus (Pc)	End. mesohumic	Humid tropics	Worldwide
Balanteodrilus pearsei (Bp)	End. Poly-mes.	SE Mexico	Regional
Diplotrema murchiei (Dm)	End. Poly-mes.	SE Mexico	Regional
Phoenicodrilus taste (Pt)	End. polyhumic	SE Mexico	Regional
Lavellodrilus parvus (Lpa)	End. polyhumic	SE Mexico	Regional
Protozapotecia australis (Pa)	End. polyhumic	SE Mexico	Regional
Eminoscolex lavellei (El)	End. polyhumic	Rwanda	Regional
Stuhlmannia variabilis (Sv)	End. mesohumic	Rwanda	Regional
Gordiodrilus sp1 *(Gg)*	End. polyhumic	Rwanda	Regional
Dichogaster itoliensis (Di)	Anecic	Rwanda	Regional
Onychochaeta elegans (Oe)	End. mesohumic	Cuba, Caribbean	Regional

Onychochaeta windelei (Ow)	End. mesohumic	Cuba, Caribbean	Regional
Pontoscolex spiralis (Ps)	End. mesohumic	Lower Antilles	Regional
Chuniodrilus zielae (Cz)	End. polyhumic	Lamto, Ivory Coast	Regional
Chuniodrilus palustris (Cp)	End. polyhumic	Lamto, Ivory Coast	Regional
Hyperiodrilus africanus (Ha)	Epiendogeic	Tropical Africa	Regional
Lampito mauritii (Lm)	Anecic	India, SE Asia	Regional
Drawida paradoxa (Dpa)	End. mesohumic	Karnataka, India	Regional
Drawida ampullacea (Damp)	Endogeic	Karnataka, India	Regional
Drawida willsii (Dw)	Epianecic	Karnataka, India	Regional
Drawida nepalensis (Dn)	End. mesohumic	Karnataka, India	Regional
Karmiella karnatakensis (Kk)	End. poly-mes.	Karnataka, India	Regional
Megascolex konkanensis (Mk)	Endogeic	Karnataka, India	Regional
Eutyphoeus incommodus (Ei)	Anecic	Northern India	Regional
Ramiellona strigosa (Rs)	End. mesohumic	Chiapas, Mexico	Local
Zapatadrilus sp.nov *(Zsp)*	Endoanecic	Veracruz, Mexico	Local
Rhinodrilus pashanasi (Rp)	End. mesohumic	Peru, Yurimaguas	Local
Millsonia anomala (Ma)	End. mesohumic	Lamto, Ivory Coast	Local
Millsonia lamtoiana (Ml)	Anecic	Lamto, Ivory Coast	Local

soil organisms. This aspect, linked to the issue of the functional value of biodiversity, is considered in Chapters 4 and 5.

The main conclusion of this survey is that native species are found frequently in tropical agroecosystems, particularly in some countries (e.g. India) where apparently low-input agricultural techniques prevail (see Chapter 2 for more on this point), or in localities with low annual precipitations that do not permit the invasion of exotics (such as Mexican localities with annual precipitations below 1300 mm, where the native endoanecic *Zapatadrilus* sp.nov1 dominates and no mesohumic exotics have been able to establish). Taking into account the fact that several native species survive in agroecosystems at a very local level (Table 1.4), the number of species to be manipulated in tropical farming systems turns out to be considerably greater than the 10–15 major exotic species identified in Table 1.1. In this regard, and at least for tropical regions, it is no longer possible to maintain Lee's (1987) statement that only exotic species are important in agricultural lands. In addition, it is highly probable that the number of native species with potential for management in agroecosystems will increase as a function of the intensity of sampling effort.

So far, we have presented the list of earthworms with potential for manipulation in tropical soils. In agricultural lands, however, manipulation practices should be considered at the community level, because mixtures of species are generally more common than single species. In the next chapter, we will analyse these species assemblages in relation to their ecological and agricultural determinants and potential for manipulation.

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2

Earthworm Communities of Tropical Agroecosystems: Origin, Structure and Influence of Management Practices

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Summary

Data of 145 and 69 earthworm communities from managed and natural ecosystems, respectively, of four continents and 15 tropical countries were analysed. The aim of the study was to separate the influence of phylogenetic, environmental and agricultural factors on the structure of earthworm communities in agroecosystems, and to evaluate their relative importance in the whole soil macrofauna community. Earthworms comprise 40–90% of macrofaunal biomass in most ecosystems except for annually cropped systems.

Three major conclusions were drawn from the analysis of community structure (regional analysis): (i) crops were, independently of region, characterized by a loss of native species and by the dominance of exotic endogeics; (ii) pastures were highly heterogenous in terms of native or exotic species dominance; (iii) native species survived better in management ecosystems of India and Africa than in Mexico–Central America.

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Local analysis in selected countries indicated that, as a general rule, the intensity of agricultural practices is negatively correlated with the amount of native species and the total abundance and biomass of earthworms; the only exception was found in the conversion of savannas to pastures, in Colombian llanos.

Introduction

In Chapter 1, a small set of earthworm species that frequently occur in tropical agroecosystems was listed. These species, both natives (widespread and locally distributed) and exotics, were found commonly in a variety of agroecosystems in different countries of the humid tropics. Selection of these species was made on the basis of frequency, without considering other attributes of populations (abundance, biomass or dominance) and communities (number of species, ecological categories). In this chapter, we first discuss the relative importance of earthworms in macrofauna communities, across a wide range of types of land use and sites from four continents. Earthworm communities from four main tropical regions are then described, with emphasis on the effects of different types of land use on structure and diversity. Finally, worldwide comparisons are made in order to discriminate between influences of phylogenetic, environmental and anthropogenic constraints on the structure of these communities.

Determinants of earthworm communities

Earthworm communities are the result of interactions between environmental variables and biological processes occurring over a long time span. The particular species assemblages that we observe in any community reflect selective (predation, competition, mutualism, etc.), stochastic (e.g. sudden unpredictable changes of weather) and historical forces (Ricklefs and Schluter, 1993). In addition, migrations, invasions and extinctions confer a dynamic status on these systems.

Although these communities have not been fully characterized, the following generalizations are observed: (i) a similar number of species in tropical and temperate ecosystems (between 13 and 17 species) (Lavelle, 1983); and (ii) separation of species into a few ecological groups, which represent particular adaptations developed to survive in litter (epigeics), soil (endogeics) or both (anecics). The predominance of one or other ecological group is determined by a hierarchical suite of environmental factors (Lavelle, 1983; Fragoso and Lavelle, 1992). Temperature appears at the higher level of determination, followed by resource availability (soil nutrient richness) and seasonal variation of humidity (Fragoso and Lavelle, 1992). In general, epigeics predominate in colder environments whereas, in the tropics, communities are dominated by endogeics. In tropical regions, where soil temperature generally remains constant, endogeic communities can shift to epigeic communities if soil nutrients and seasonality of rains are low (Fragoso and Lavelle, 1992). Soil organic matter content also influences earthworm communities, by dividing endogeics into groups that feed on rich (polyhumic), medium (mesohumic) or poor (oligohumic) substrates (Lavelle, 1983). More details on the defintion of these ecological groups are given in Lavelle (1988) and Fragoso *et al.* (1997). Phylogenetic constraints could also play a role, because it seems that epigeic communities are more frequent in South American and African soils than in Central American soils.

When natural forests and/or savannas are destroyed and substituted by agroecosystems, the original earthworm communities are modified. Changes can occur at the taxonomical (e.g. substitution of stenoecic natives by exotics and/or euryoecic natives – see Chapter 1), ecological (e.g. increase or decrease in number of species, abundance or number of ecological categories) or both levels.

The main objective of this chapter was to find the patterns and/or rules in the assemblage of earthworm communities in agroecosystems, and to answer the following questions:

1. What is the relative importance of earthworms in macrofaunal communities?
2. What is the importance of phylogenetic constraints for the structure of earthworm communities?
3. How does community structure respond to different types of land-use practices?
4. To what extent do communities retain effects of past disturbances (cropping, application of chemicals, time elapsed)?
5. To what degree does the original natural community determine the structure of the agroecosystem community?

Analysis of Data and Regions

Earthworm community data from a variety of countries and regions throughout the humid tropics were obtained from literature reviews and field sampling. In the first case, data were taken from several localities in Mexico (Fragoso and Lavelle, 1987, 1992; Fragoso, 1989, 1992, 1993; Arteaga, 1992), Costa Rica (Fraile, 1989), Lesser Antilles (Barois *et al.*, 1988), Peru (Lavelle and Pashanasi, 1988, 1989; Rombke and Verhaagh, 1992), Colombia (Decaëns *et al.*, 1995), Ivory Coast (Lavelle, 1978; Tondoh, 1994; Gilot *et al.*, 1995), Congo (Montadert, 1985; M'Boukou, 1997), India (Dash and Patra, 1977; Kale and Krishnamoorthy, 1978; Chaudry and Mitra, 1983; Julka and Mukherjee, 1984; Krishnamoorthy, 1985; Mishra, 1986; Pani, 1986; Julka and Senapati, 1987; Mohanty, 1988; Bhadauria and

Ramakrishnan, 1989; Julka *et al.*, 1989; Ismail *et al.*, 1990; Bano and Kale, 1991; Darlong and Alfred, 1991; Blanchart and Julka, 1997) and Venezuela, Malaysia and Sarawak (Fragoso and Lavelle, 1992). Additional sampling was conducted in Mexico (Ortiz and Fragoso, unpublished), India (Senapati *et al.*, unpublished), Cuba (Martinez, unpublished) and Colombia (Jimenez, unpublished). In total, we analysed 214 sites from 63 localities within 15 tropical countries. Of these numbers, 145 sites were tropical agroecosystems and 69 natural ecosystems. Table 2.1 shows the classification of these sites by country and land-use system; this table also indicates the type of community data. All data were stored in EWDBASE (see Chapter 1).

In order to discriminate between the influence of history (phylogenetic lineages) and environmental–anthropogenic influence (natural and managed ecosystems), communities were separated into four regions and eight major vegetation types. The regions were Asia (India, Sarawak, Malaysia), Africa (Ivory Coast, Congo), Central America (Mexico, Cuba, Lesser Antilles, Costa Rica) and South America (Peru, Colombia, Brazil and Venezuela). The types of vegetation were tropical rainforests (below 1000 m of altitude and annual precipitation over 2000 mm), tropical subdeciduous forests (below 1000 m of altitude and annual precipitation between 900 and 1800 mm), savannas, temperate forests (including cloud, *Eucalyptus*, pine and oak forests over 1000 m of altitude), fallows, crops (including maize, sugar cane, yam, tea, peanuts), pastures, grasslands and tree plantations (including coffee, rubber, banana, mango). Principal component analysis (PCA) was carried out (STATGRAPHICS software) with the following community variables: abundance, biomass and number of species for total, native, exotic, epigeic, endogeic and anecic species.

In order to place earthworm communities correctly in the overall context of soil macrofauna, we used the results obtained by Lavelle *et al.* (1994) for analysis of soil macrofaunal composition, where 73 macroinvertebrate communities from 29 different sites were studied. The importance of each group (Oligochaeta, Formicidae, Isoptera, Aranae, Chilopoda, Diplopoda, Diptera, Aranae, Gasteropoda, Coleoptera) was determined according to their relative contribution to total density and biomasss, for each one of the above-mentioned types of vegetation.

General Patterns of Macroinvertebrate Communities

Tropical soil macrofauna trends

Lavelle *et al.* (1994) identified, by PCA, the major trends in tropical soil macrofaunal composition and the relative effect of vegetation type, biogeography and land-use practices.

Table 2.1. Origin, type of land management and number of earthworm communities analysed in this study.

	Natural ecosystems					Agroecosystems			
Country	No. of localities	Tropical forests	Cloud forests	Temperate forests	Savannas	Pastures	Tree plantations	Fallows	Crops
America									
Brazil	1	1[a]	—	—	—	3[a]	1[a]	—	—
Colombia	2	3[a,b]	1	—	1[a,b]	3[a,b]	2[a,b]	3[a,b]	2[a,b]
Costa Rica	3	2[a]	—	—	—	4[a,b]	—	—	—
Cuba	1	1[a]	—	—	—	1[a,b]	1[a,b]	—	—
Dominica	1	—	—	—	—	1[a]	1[a]	—	—
Guadaloupe	1	—	—	—	—	2[a]	—	—	3[a]
Martinique	1	—	—	—	—	3[a,b]	1[a,b]	—	—
Mexico	23	12[a,b]	2[a,b]	1[a,b]	—	18[a,b]	3[a,b]	2[a,b]	10[a,b]
Peru	2	3[a,b]	—	—	—	3[a,b]	1[a,b]	2[a,b]	3[a,b]
Venezuela	1	3[a,b]	—	—	—	—	—	—	—
Africa									
Congo	1	4[a,b]	—	—	—	1[a,b]	1[a,b]	—	—
Ivory Coast	3	3[a,b]	—	—	6[a,b]	2[a,b]	5[a,b]	3[a,b]	11[a,b]
Asia									
India	21	19[a,b]	—	—	—	26[a,b]	9[a,b]	3[a,b]	11[a,b]
Malaysia	1	3[a]	—	—	—	—	—	—	—
Sarawak	1	4[a]	—	—	—	—	—	—	—
Total	63	58	3	1	7	67	25	13	40

[a] Density and/or biomass data available; [b] ecological categories identified.

The major outcome of this analysis was the identification of three major groups characterized respectively by the dominance of either termites, earthworms or litter arthropods. The groups tend to react separately within ecosystem types and land-use practices. Termites and/or earthworms tend to be dominant in most cases, while termite communities vary widely, depending on biogeographical patterns. They are important components of many African and Australian soils. In America, ants are more important whereas termites often are of little or no importance. This is due, in part, to their lower functional diversity; in South America for example, fungus-growing termites do not occur. Another important characteristic of termites is that they have adapted to a wide range of semi-arid systems where earthworms are not found. Earthworms are best represented in grasslands in humid areas; their abundance decreases towards both forested and dry areas. At a finer level of resolution, they are sensitive to the nutrient status and organic content of soil (Fragoso and Lavelle, 1992). Litter arthropods seem to be predominant in ecosystems where sufficient litter is available as a consequence of low termite and earthworm activities. They are represented mainly by millipedes or coleopterans, which in some areas account for the larger part of the biomass, as in the case of millipedes in the miombo woodlands of southern Africa (Dangerfield, 1990). In such ecosystems, mesofaunal communities may also have higher densities than in systems dominated by earthworms and termites, where their abundance is very low (Adis, 1988).

Effect of land-use practices

Annual crops on land recently cleared of natural vegetation always have highly depleted macro-invertebrate communities (Fig. 2.1). They have the lowest biomass (5.1 g of fresh weight m^{-2} on average) and a very low diversity. Earthworm and litter arthropod populations soon disappear, as native species seldom withstand major disturbances, provided they are not replaced by adaptable exotic species. Some groups of termites (mainly humivorous) tend to be more persistent and comprise a significant proportion of the overall biomass.

Pastures are functionally similar to savannas. They are highly favourable for earthworm development when they have been established in forest areas with high annual rainfall, provided adaptable species are present. This is actually the case in many sites where peregrine species with pantropical distributions (mainly *Pontoscolex corethrurus* and *Polypheretima elongata*) establish biomasses from several hundreds to 4000 kg of fresh weight per hectare (see, e.g. Barois *et al.*, 1988; Lavelle and Pashanasi, 1989). However, in some cases (India and Mexico), native species can survive, reaching similar abundance values. Interestingly, sugar cane plantations show similar patterns, with earthworm biomasses of 33 and 53 g m^{-2} in two sites in tropical Mexico and Guadeloupe, respectively (Barois *et al.*, 1988; Patrón, 1993). In terms of

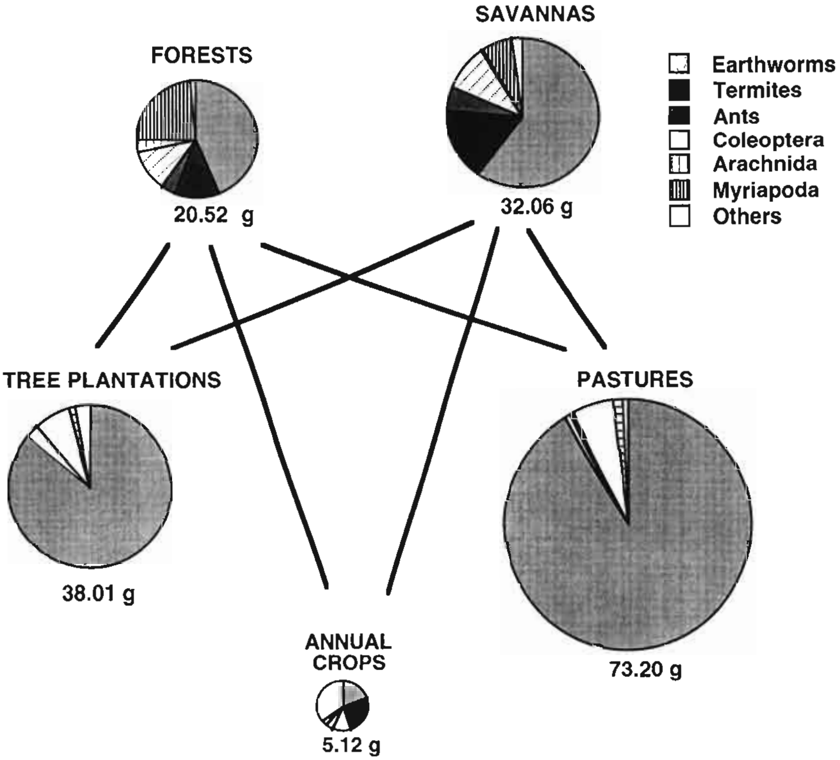

Fig. 2.1. Composition of soil macrofaunal communities in tropical grasslands, fallows + tree plantations, annual crops and forests. The area of circles is proportional to the overall biomass.

soil–fauna relationships, this indicates that these plantations are comparable with humid grasslands.

Tree plantations such as palm tree plantations with herbaceous legume cover, or cocoa with a litter layer at the soil surface and a stratum of high trees, usually have diverse communities. They retain components of the original fauna because some of the original species are still present as the overall structure is close to that of a secondary forest. Nonetheless, the disturbance and/or the establishment of a herbaceous stratum provides niches that allow some exotic species to colonize.

Species richness and diversity

Although no really comprehensive information is available so far, disturbances linked to land-use practices seem to severely affect the species richness of soil arthropod communities. The conversion of forests to annual crops eliminates the vast majority of species which rely on woody or leaf litter material and those which need buffered microclimatic conditions. Conversely, perennial systems, especially those which maintain a multistrata structure, may conserve species from the original ecosystem and provide niches for exotic colonizers. The nature of the original ecosystem greatly influences the effect of land-use practices. In Colombia, conversion of savannas into pastures generally maintains a large part of the original community (54% of species in common), with some changes induced by grazing. In contrast, in a pasture established at Manaus after clearing the forest, species richness of macroinvertebrate communities had decreased from 151 to 48 species, and only 22 from the original communities had resisted the change (22.5% of species in common).

Earthworm Communities of Tropical Agroecosystems

Regional analysis

Here we present the patterns of earthworm communities from several tropical countries. These countries are grouped according to their biogeographic and phylogenetic affinities into four regions: (i) Central America–Caribbean; (ii) South America; (iii)Africa; and (iv) Asia.

Central America and the Caribbean

This region is characterized by the presence of primitive Megascolecidae (Acanthodrilinae and Dichogastrini), Ocnerodrilidae and some derived Glossoscolecidae distributed in the major part of Mexico, Central America (north of Panama) and the Lesser and Greater Antilles. It includes more than 130 species and 25 genera (Fragoso *et al.*, 1995). Only in Mexico, Cuba, some Lesser Antilles and Costa Rica have natural and/or agroecosystem earthworm communities been characterized.

MEXICO

We will restrict case studies to southeastern Mexico, currently considered as the most humid region of the country and very rich in native species (Fragoso and Rojas, 1994). In this region, 48 earthworm communities (15 in natural ecosystems and 33 in agroecosystems) from 23 localities were characterized. Most of the following results are from Fragoso *et al.* (1997.)

With a surface of nearly 488,000 km^2, more than half of the original vegetation of this region has been replaced by agroecosystems; the remaining natural vegetation (tropical rainforests, deciduous and subdeciduous forests) is sparsely distributed over the entire region. Pastures and cultivated lands are the predominant agroecosystems, occupying more than 30% of the total surface of the region (Fragoso, 1993).

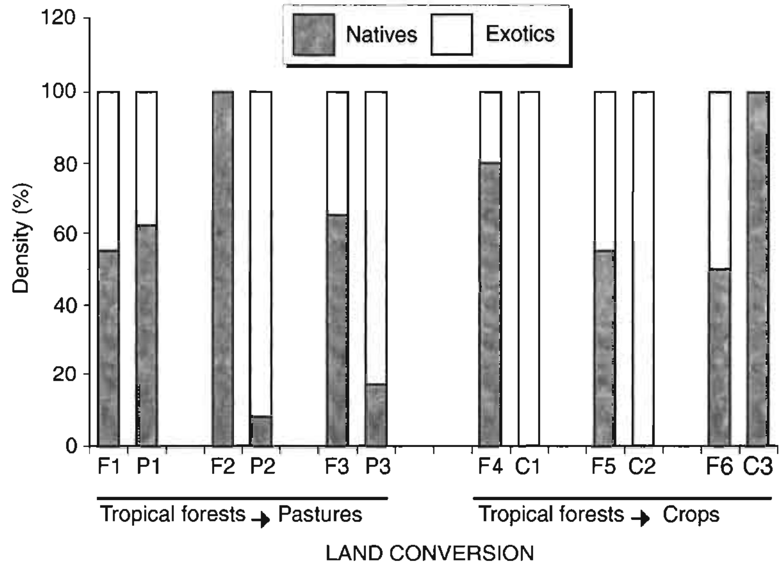

Fig. 2.2. Change of earthworm community composition in different land-use systems of southeastern Mexico. F = forests, P = pastures, C = annual crops. See text for the meaning of numbers. (Modified from Fragoso *et al.*, 1997.)

The current number of species in this region is 95, of which 26 are exotics (Fragoso, 1993). Regional richness (i.e. the total number of species living in a certain type of ecosystem from different geographical localities) is higher in tropical forests (40 species) than in pastures (22 species) and maize crops (15 species); conversely, the area of pastures is almost twice that of tropical forests. From a regional point of view, this means that: (i) with the destruction of natural forests, many native species disappear at the local scale, and (ii) 50% of disturbed below-ground areas of southeastern Mexico are inhabited by a small number of earthworm species (mainly exotics).

The general pattern in this region is that earthworm communities of natural and disturbed ecosystems are composed, to some extent, of a mixture of native and exotic species. The structure of these communities varies greatly with the nature of soil management. In general, communities from natural ecosystems show lower abundances and biomasses than those from disturbed sites; the exception are crops (mainly maize) which present lower values of density, biomass and number of species (average values 42 ind m^{-2}, 1 g m^{-2} and 2 species m^{-2}, respectively). In both natural and disturbed ecosystems, endogeics dominate, indicating that epigeic species are not an important component in Mexican natural earthworm communities, and thus perturbation has a smaller effect on functional diversity. It was also demonstrated that when the community includes the exotics *P. corethrurus* or *P. elongata* (these species seldom coexist in the same site), they are generally dominant. Other common assemblages found in this region include the exotics *P. corethrurus*, *Dichogaster* *bolaui* and *D. saliens* and the euryoecic natives *Balanteodrilus pearsei*, *Lavellodrilus parvus* and *Diplotrema murchiei*.

After comparing the structure of earthworm communities in several agroecosystems, Fragoso (1993) found that the two more important determinants of these communities were the time of disturbance (which measures time elapsed since first perturbation) and the kind of agricultural practices (amount and intensity of soil destructive agricultural practices, e.g. use of tillage, pesticides, fertilizers). Figure 2.2, for example, shows that in recently disturbed pastures (P1, Chajul; Fragoso, 1992) and crops with low-input agricultural practices (C3, Pánuco; Arteaga, 1992), natives remain as an important component; the use of high-input agricultural practices (tillage, pesticides) in combination with a longer time elapsed since perturbation increased the amount of exotics both in pastures (P2, Los Tuxtlas; Fragoso, 1993; P3, Laguna Verde; Lavelle *et al.*, 1981) and in crops (C1, Gómez Farías; C2, La Mancha; Fragoso, 1993).

CUBA

The largest of the Caribbean islands, Cuba harbours a very diverse earthworm fauna. However, there has only been one study in which earthworm communities of agroecosystems have been analysed in relation to natural vegetation (Martínez, unpublished data). Comparisons made at La Habana between tropical subdeciduous secondary forests, pastures and tree plantations indicated that: (i) endogeics dominated (100% of total abundance and biomass) in the tree sites; (ii) higher values of density and biomass were found in forests (413 ind m^{-2} and 170 g m^{-2}) followed by pastures (338 ind m^{-2} and 174 g m^{-2}); (iii) species richness was higher in pastures (seven species) followed by forests (five species); (iv) the most important species in the three systems was the widespread native *Onychochaeta elegans*; and (v) in the two agroecosystems, the second most important species was the exotic *P. elongata*.

LESSER ANTILLES

Barois *et al.* (1988) studied the soil macrofauna and earthworm fauna of different land-use systems from Guadaloupe, Dominica and Martinique. In the first two islands, the exotic *P. corethrurus* was relatively abundant in several kinds of agroecosystems, with some native species scarcely represented; in vertisols of Martinique, on the other hand, the exotic *P. elongata* totally dominated the communities of pastures and other agroecosystems.

COSTA RICA

Fraile (1989), in the only study so far in Costa Rican tropical agroecosystems, analysed earthworm communities in pastures with different treatments of fertilizers and agroforestry techniques. This author found the highest values of abundance, biomass and species richness in a non-grazed pasture (226 ind m^{-2}, 67 g m^{-2} and nine species) and, for all the treatments, an overwhelming dominance of the exotic *P. corethrurus*. In general, epigeics were scarce, the higher values (2% of total biomass) being found in pastures with *E. poeppigiana* trees (mainly the exotic *Metaphire californica*). Only one native species survived (*Glossodrilus nemoralis*) and with very low values of abundance. Thus, intensive management, as in the case of Mexico, affected abundance and species composition.

South America

Although the families Ocnerodrilidae and Megascolecidae also occur in this region, the distinctive feature in this continent is the dominance of family Glossoscolecidae. With 36 genera recognized (Righi, 1996) and hundreds of species distributed both in tropical and temperate ecosystems (except the southern region of Chile and Argentina; Righi, 1971), members of this family often dominate the earthworm communities so far studied in Peru, Brazil and Colombia.

PERU

Lavelle and Pashanasi (1988, 1989) compared earthworm communities from two tropical rainforests with three groups of derived agroecosystems. Their results showed that earthworm communities were modified both at the functional and taxonomic level (Fig. 2.3). Functionally there were changes in the amount and kind of ecological groups; in the majority of the sampled agroecosystems, for example, the community structure was greatly simplified, often to only one ecological category. Structural changes were clear in pastures, fallows and high-input cropping systems, where the forest earthworm communities shifted from an epigeic- to an endogeic-dominated composition; taxonomically, the four original native forest earthworm species were almost totally replaced by the exotic *P. corethrurus*.

Interestingly, as occurred in southeastern Mexico, epigeic and anecic native species remained in palm tree plantations (Pijuayo-kudzu) and in traditional and low-input cropping systems.

In another set of experiments, Pashanasi *et al.* (1994) followed changes in the composition of earthworm communities, from recently burned forest to shifting cultivation and improved agriculture. After the first harvest in both systems, they found that the native epigeic species *Martiodrilus pano* completely disappeared, while populations of the native anecic *Rhinodrilus lavellei* and the endogeic *Rhinodrilus pashanasi* species were maintained and increased, respectively.

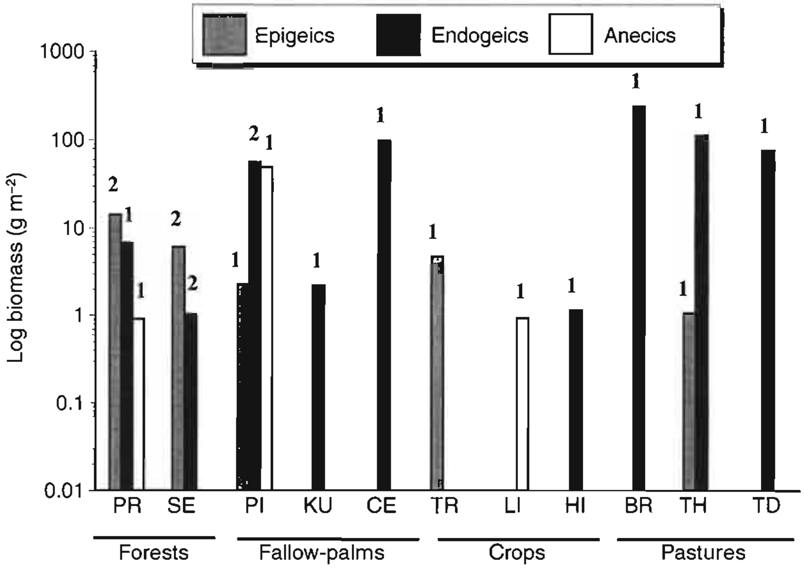

Fig. 2.3. Functional (ecological categories) and taxonomical (number of species) changes of earthworm communities in different land-use systems in Peruvian Amazonia. Values above the bars indicate the number of species in each category (from Fragoso *et al.*, 1997). BR = *Brachiaria*, CE = *Centrosema*, HI = high input, KU = Kudzu, LI = low input, PI = Pijuayo, PR = primary, SE = secondary, TD = traditional dry, TH = traditional humid, TR = traditional.

BRAZIL

At Manaus, Lavelle *et al.* (unpublished data) found pastures and forests with similar values of biomass (approx. 44 g m^{-2}). Density, on the other hand, showed higher values in pastures (602 ind m^{-2} versus 202 ind m^{-2} in forests). The main difference between these systems was the disappearance of native earthworms and the colonization of presumably empty niches and building up of large populations by the exotic species *P. corethrurus*. Dominance of this species and a drastic reduction in other invertebrates resulted in a decompacting effect on soil, which in turn produced a significant degradation of soil physical structure (see Chapter 5).

COLOMBIA

At Carimagua, conversion of savannas into improved pastures with African grasses and herbaceous legumes increased the abundance and biomass of earthworm communities and maintained a large proportion of native species.

Of the eight earthworm species recorded in the original savanna, seven were maintained in improved pastures and the overall earthworm biomass was increased five- to 12-fold (from 4.78 g m^{-2} in the original savanna to 51 g m^{-2} in the improved pasture; Decaëns *et al.*, 1994). Exotic species present in the area did not invade the pastures. The positive effect of improved pastures on native earthworms was reflected in the anecic glossoscolecid *Martiodrilus* sp.nov. In the native savanna, this large species comprised up to 15.1% of total earthworm biomass, whereas in the improved pasture this value increased to 85.1% (Jimenez *et al.*, 1998).

Africa

The earthworm fauna of this continent is represented by ancestral taxa of Megascolecidae and derived Eudrilidae and Microchaetidae. Particularly abundant in Central Africa is the family Eudrilidae, which actually includes 38 genera and more than 274 species (Sims, 1987). In general, earthworm communities contain a mixture of megascolecid [mainly *Dichogaster* or related species with calciferous glands in the region 14–17, grouped by Csuzdi (1996) in the distinctive subfamily Benhamiinae] and eudrilid species. Community studies have been made up to now only in Ivory Coast and Congo.

IVORY COAST

Lavelle (1978) studied several earthworm communities from different types of savannas and gallery forests at Lamto. Their studies revealed rich (up to 13 species) and ecologically diverse communities (in particular the endogeics) flourishing in very poor sandy soils. Interestingly, when these natural systems were shifted to some kind of agroecosystem, none of the exotic species invaded these communities. Tondoh (1994) characterized earthworm populations from several land-use systems that included natural unburned forests, burned forests, savannas and a variety of cultures with different intensities of agricultural practices and ages of disturbance (Fig. 2.4). Their results showed the polyhumic eudrilids *Chuniodrilus* spp. and the megascolecid endogeic *Millsonia anomala* and *Dichogaster agilis* as the only species capable of survival in these systems. The persistence of original earthworms varied with the kind of culture, soil moisture and age of cultures. Very humid agroecosystems (e.g. rice, banana plantation) showed higher total abundances and biomasses than adjacent gallery forests, whereas in maize crops the community changed with age from mesohumic (maize for 1 year, dominated by *M. anomala*) to epigeic-dominated communities (maize for 3 years, dominated by *Dichogaster* spp.). Finally, in a pasture established in a former natural forest, the number of species remained the same although biomass never reached the values found in natural savanna communities (Fig. 2.4). In summary, this study showed that: (i) endogeic earthworms dominate both in natural and managed systems; (ii) exotics never invaded derived communities; and (iii) agroecosystem communities changed their functional structure with time.

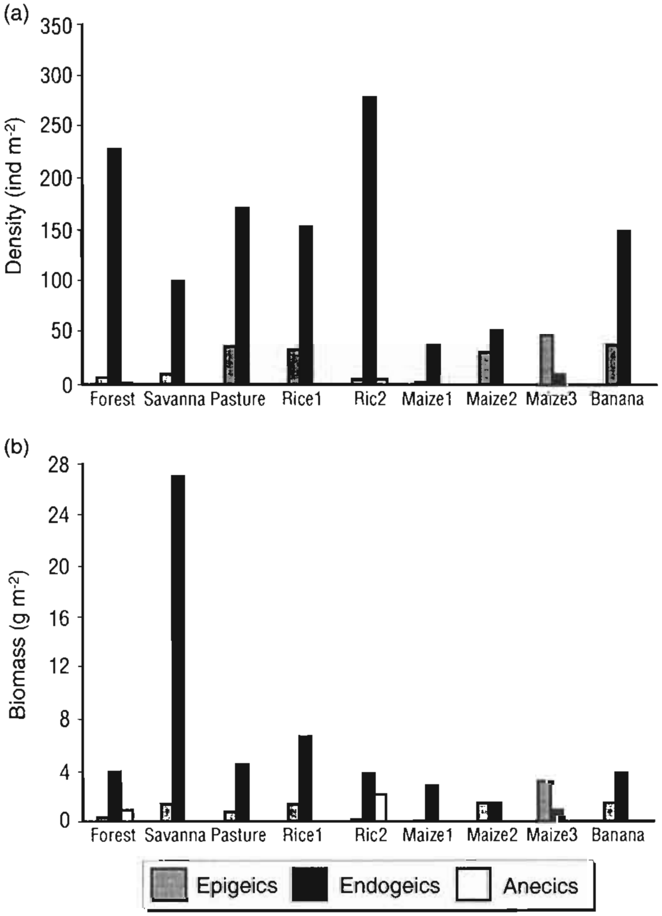

Fig. 2.4. Abundance (a) and biomass (b) of earthworm ecological groups in different land-use systems from central Ivory Coast (Tondoh, 1994). Numbers on the *x*-axis indicate number of years

CONGO

Montadert (1985), working in forests and derived agroecosystems of Dimonika, found that both pastures and cacao plantations showed higher abundance and biomass values than natural forests. The situation in pastures, however, was similar to that found in other American sites: an almost total domination of *P. corethrurus*.

The Maala system investigated in the Niari Valley (M'Boukou, 1997), on the other hand, is an interesting exception to the general patterns observed elsewhere. It is actually the only annual cropping system that enhances earthworm communities. Annual crops are grown on mounds in which grass

Table 2.2. Earthworm density (D) (ind m^{-2}) and biomass (B) (g m^{-2}) in different land-use systems of the Niari region (Congo).

	Savanna D (B)	Slash-and-burn D (B)	Maala 1st year D (B)	Maala 2nd year D (B)	Maala 3rd year D (B)
Epigeics	18 (6)	5 (0.42)	31 (9)	37 (17)	16 (5.3)
Anecics	0	0	33 (12)	11 (4.3)	0
Endogeics	61 (19)	13 (2)	363 (139)	146 (30)	138 (4)
Total m^{-2}	79 (25)	18 (2.42)	427 (160)	194 (51.3)	154 (9.3)

previously had been buried and slowly burned. This practice keeps ashes and a significant proportion of carbon in the soil, with positive effects on earthworm abundance. As shown in Table 2.2, earthworm density decreased from 79 to 18 ind m^{-2} in the slash-and-burn system, whereas in the Maalas earthworm density increased more than fivefold and biomass reached 160 g m^{-2} during the first year. Endogeics and anecics were stimulated more than epigeics. Earthworm abundance and biomass decreased during the second and third year, but the former still remained higher than in the savanna. Functionally, the Maala system enhanced the invasion of anecics, which were not present in the savannas.

Asia

The Asiatic earthworm fauna is dominated by species of Megascolecidae (Megascolecinae, Dichogastrini and Peryonichini), the primitive Moniligastridae and some Ocnerodrilidae (Edwards and Bohlen, 1996). Within the Megascolecinae, the most diverse and successful group of earthworm species is found: the pheretimoid-related genera (*Pheretima, Polypheretima, Metaphire, Amynthas,* etc.), that include several of the tropical common exotic species (see Chapter 1). From a phylogenetic point of view, this region has strong affinities with Africa and Central America. Notwithstanding their surface and high diversity of species, detailed studies of tropical earthworm communities in this continent have only been carried out in India.

INDIA

India covers only about 2% of the world's total surface, but with 385 species and 64 genera recognized it harbours about 10% of all known earthworm species (Julka, 1999). Earthworm community research in this country has been carried out both at the regional (21 localities) and local level, both in natural (19 sites) and derived agroecosystems (49 sites, Table 2.1).

Changes in earthworm communities are exemplified by the studies carried out in southern Karnataka (Deccan Peninsula) by Bano and Kale (1991) and Blanchart and Julka (1997). In the regional study, Bano and Kale (1991) reported 44 species (36 natives and eight exotics), of which seven and 25 native species were limited to natural forests and managed ecosystems, respectively. Figure 2.5a shows that native species are well adapted to agroecosystems, surviving even in arable lands. That more native species were found in managed ecosystems than in natural forests could be due to: (i) the wide geographical distribution of the majority of natives (widespread natives of Chapter 1), (ii) the prevalence in the region of low-input agricultural practices (Kale, personal communication) and (iii) the fact that most of these earthworms were endogeic species, which are more resistant to changes in land-use practices. In a more local study in the same region, Blanchart and Julka (1997) studied earthworm communities in a gradient of forest disturbance (forest–forest borders–pastures). Their results can be summarized as follows: (i) communities were composed mostly of endogeic species (only one epigeic

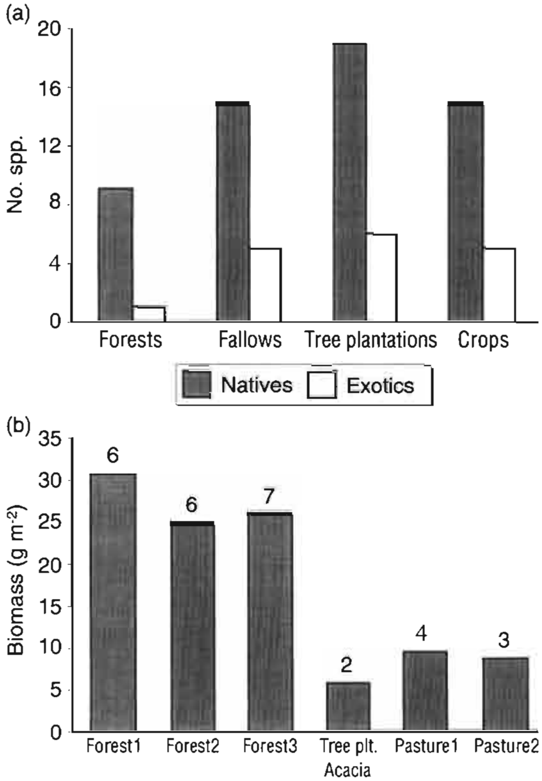

Fig. 2.5. (a) Number of native and exotic species from different land-use systems in southern Karnataka, India (data from Bano and Kale, 1991). (b) Biomass of earthworms found in different land-use systems from the Western Ghats, Karnataka state, India. Values above the bars indicate the number of species (data from Blanchart and Julka, 1997). Numbers of land-use systems are shown only to separate sites.

species from a total of 30 species); (ii) more than 60% of species survived in at least one type of agroecosystem; (iii) no globally distributed exotic species were found; and (iv) lower values of abundance, biomass and species numbers were found in pastures, as opposed to natural forests (Fig. 2.5b).

These examples are representative of the situation currently found in other Indian localities, that can be summarized as follows:

1. In almost all kinds of agroecosystems, earthworm communities are composed mainly of native species which generally dominate in abundance and biomass (e.g. several species of *Drawida*, *Hoplochaetella*, *Eutyphoeus*, *Lennogaster*, etc.; see Chapter 1).
2. The exotics *P. corethrurus* and *P. elongata* are uncommon. In fact, India is the only country in which native species are very common at local and regional levels, not only in pastures but also in tree plantations and crops (Fig. 2.5a). The presumed cause of this pattern is, as in southeastern Mexico, the limited use of mechanized destructive agricultural practices.

A synthesis of regional and worldwide patterns of natural and disturbed tropical earthworm communities

The above case studies show that when natural forests and savannas are converted to agroecosystems, earthworm communities change in abundance, biomass, number of species, ecological categories and species composition. With these data, is it possible to identify a common trend in the direction of change of these communities, and the extent to which phylogenetic–geographic constraints determine specific patterns and trends?

We explored these questions by performing a PCA with data from natural and derived ecosystems in different tropical regions. Thus, we expected to discriminate between the effect of phylogeny, environment and agriculture practices. Because not all sites were fully characterized (e.g. in some cases only abundance data were available), two kinds of PCA were performed. The first (A1) was run considering only density and species number for total, native, exotic, epigeic, endogeic and anecic groups (12 variables) and included 158 sites; the second (A2) was restricted to localities with density, biomass and species richness (18 variables and 129 sites). Standardization of data was carried out in both analyses.

In the case of A1, the first two components explained 50% of total variance (25% each), whereas for A2 the percentage of explained variance was 24 and 20% for components 1 and 2, respectively (44% together). In both analyses, components 1 (C1) and 2 (C2) were similar: they reflected the influence of exotic species, mainly endogeics, on the overall abundance and biomass (C1) and the influence of native species as determinants of community species richness (C2).

The influence of land-use systems

The result of A1 analysis is shown in Fig. 2.6, where sites were separated according to land-use system. In this figure, combinations of C1 and C2 produced four types of communities, represented in Fig. 2.6 by the uppercase letters A, B, C and D. Type A communities are characterized by high numbers of (native) species, a more diverse functional structure (several ecological categories) and low abundance values; they are found in most tropical rainforests and some pastures and savannas. In type B communities, native species richness is still high, but exotic endogeics produce high abundance values; some tropical forests, fallows, crops and several pastures are included in this group. Type C communities represent the most depauperate systems, with low values of abundance, species richness and ecological categories; in these communities, very few natives are represented and even the exotic endogeics are seldom present. Most annual crops and several pastures are included in this group. Finally, type D communities show very few native species but high abundance values due to the dominance of exotic endogeics. All sites with this kind of community correspond to agroecosystems (pastures, tree plantations and crops).

These patterns can be summarized as follows:

1. Considering all sites together, there is some overlap between natural and managed sites, which is simply due to the fact that several agroecosystems maintained their original communities. However, there are clear trends in the composition of communities according to land management. For example, from Fig. 2.6, it is concluded that 56% of natural ecosystems (all savannas and most tropical rainforest sites) are species-rich communities with low abundance values, but with an ecologically diverse native earthworm fauna (e.g. with epigeic, endogeic and anecic species) (quadrant A of central graph in Fig. 2.6). In the case of agroecosystems (fallows, crops, pastures, tree plantations), 44% of the sites are characterized by depauperate earthworm communities with low abundances and number of species (quadrant C), whereas 42% of the sites are characterized by high-abundance communities dominated by exotic endogeics, with low or high native species richness (quadrants B + D).
2. A great deal of crop sites (72%) are characterized by low abundances and low native species richness (quadrant C).
3. Pastures are very heterogeneous in terms of total abundance, dominance of exotics and species richness; in fact, it is the only land-use system which significantly conserved a diversified native fauna (48% of sites, quadrants A + B of Fig. 2.6).

Regional patterns of communities.

In Fig 2.7, the results of analysis A1 are partitioned according to geographical region. Considering the four types of communities previously recognized (A, B, C and D), the following patterns are observed:

1. In Asia, Africa and South America, more than 50% of natural sites (black bars, Fig. 2.7A) show communities with high numbers of native species and

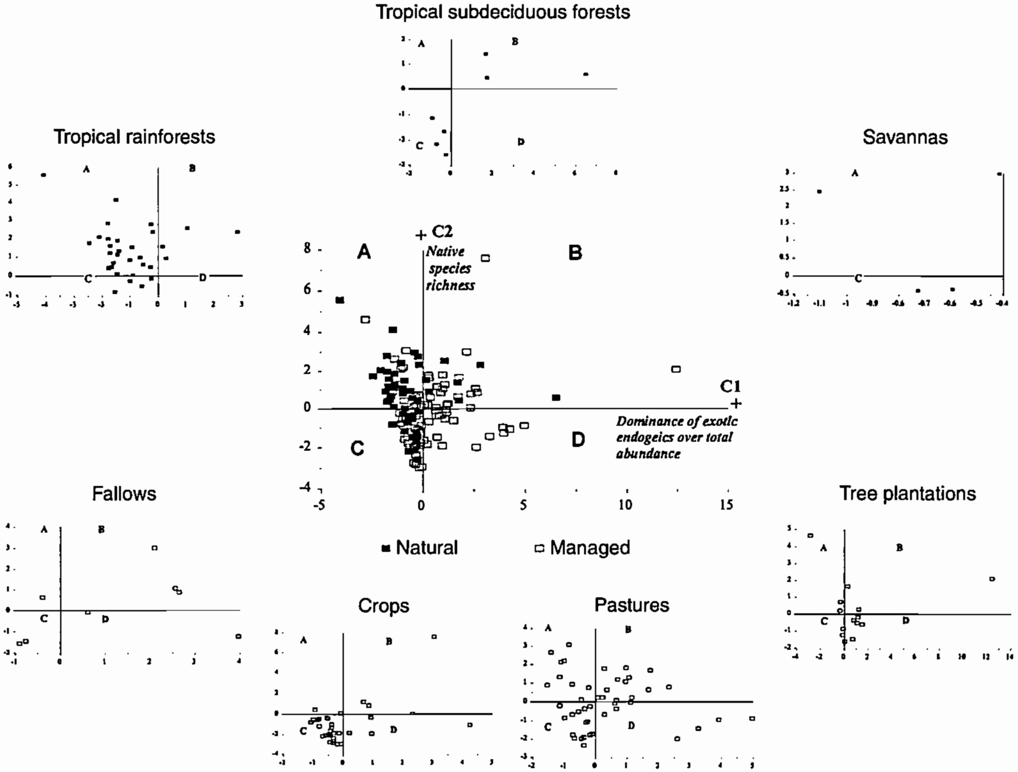

Fig. 2.6. Ordination of 140 earthworm communities from different countries of the humid tropics and separation on the basis of land-use system. Letters for each quadrant are shown only to differentiate the meaning of components and are explained fully in the text.

with a diversified functional structure (i.e. several ecological categories); in the Mexico–Central America region, on the other hand, the relatively common low-diversity communities (44% of sites; black bars, Fig. 2.7C) mainly correspond to tropical subdeciduous forests. These forests, found in localities with annual precipitation lower than 900 mm, represent the distributional limit for the majority of tropical native earthworms (Fragoso and Lavelle, 1992), and consequently are inhabited by few native species (mainly endoanecic = large endogeics with deep vertical burrows) and by the more plastic exotic endogeic species (Fig. 2.6B).

2. There is a clear difference between the agroecosystem communities of Asia–Africa and those of Mexico–Central/South America (empty bars, Fig. 2.7). In the first case, nearly 50% of agroecosystems are characterized by rich earthworm communities with several native species (Fig. 2.7 A + B), whereas in the second case this percentage decreases to 35% (Mexico–CA) and 12% (South America). This pattern indicates that in Asia and Africa, managed agroecosystems offer better conditions for the survival of native species and for the conservation of the functional structure of the community.

3. In the recent analysis by Lavelle *et al.* (1994), of 18 agroecosystems from Mexico and Peru, it was found that earthworms were more abundant in pastures than in any other agroecosystem. With more data from other countries and regions, our results indicate that this pattern only holds in tropical America and Africa; in Asia (India), traditional management practices have promoted high densities in tree plantations, equally or slightly higher than those found in pastures (more than half of the managed sites from India in Fig. 2.7D correspond to tree plantations).

The conservation of the richness and functional structure of earthworm communities in agroecosystems is related to the phylogenetic background, the type of agroecosystem (e.g. both in India and Mexico, pastures conserve several native species) and the kind of agricultural practices currently used.

The influence of phylogeny on the functional structure of these communities (measured by the relative importance of ecological categories) can be estimated by comparing natural communities from different regions. After the initial synthesis made by Lavelle (1983) and confirmed by Lavelle *et al.* (1995), it is recognized that tropical savannas and forests are dominated by endogeics, which account for more than 80% of total biomass. Fragoso and Lavelle (1992), in a more detailed analysis of several tropical rainforest communities from Mexico, Central America, Africa and South America, conclude that these communities are rather similar in terms of species richness, the main difference being the predominance of certain ecological categories. They found a predominance of anecic and epigeic species in South American and African communities; in Mexican communities, on the other hand, endogeics dominated. Their main conclusion, however, was that these patterns were the result of environmental determinants (soil nutrient contents and rainfall seasonality), rather than phylogenetic–geographic constraints related to a predominance of

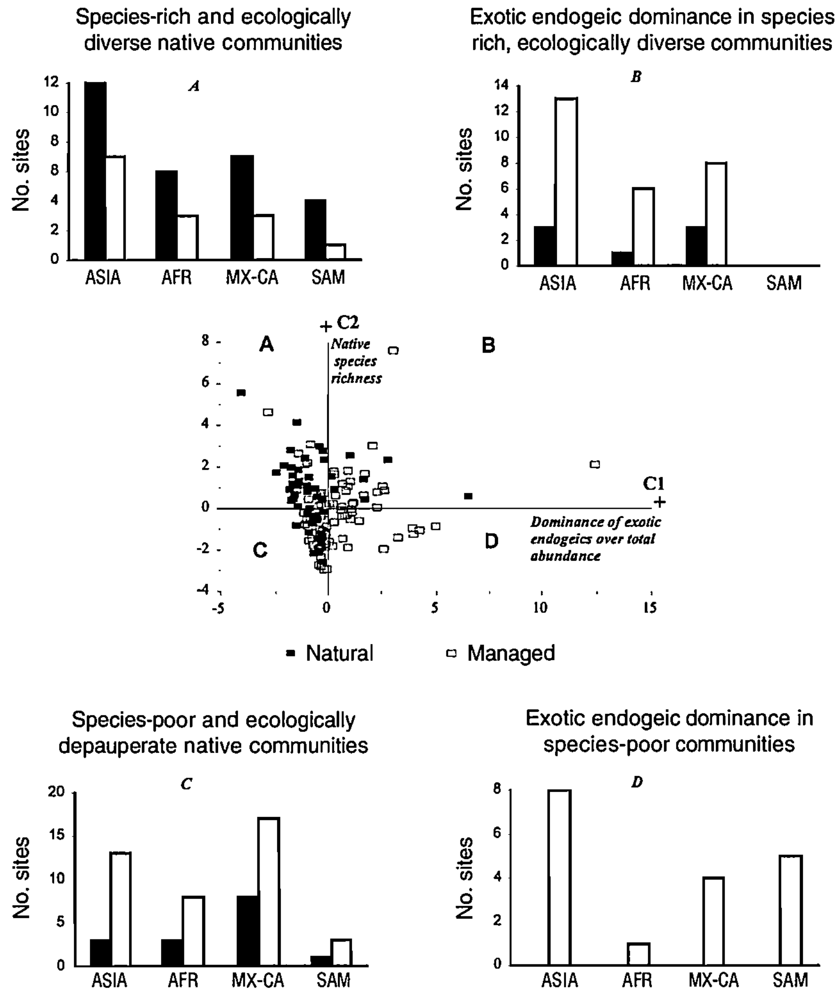

Fig. 2.7. Ordination of 140 earthworm communities from different countries of the humid tropics and separation on the basis of geographical regions (AFR = Africa, MX-CA = Mexico–Central America, SAM = South America). Bars indicate the number of natural (black) and managed (white) sites separated by components and by geographical region (see text).

epigeics and anecics in the families Glossoscolecidae (South America) and Eudrilidae (Africa). Actually, however, discrimination between both hypotheses will rely on the use of appropriate adaptive phylogenetic methods (Harvey and Pagel, 1991).

In this study, and with more data from different land-use systems, we found that the 'phylogenetic' background is important in determining the structural composition of communities, their effect varying as a function of the

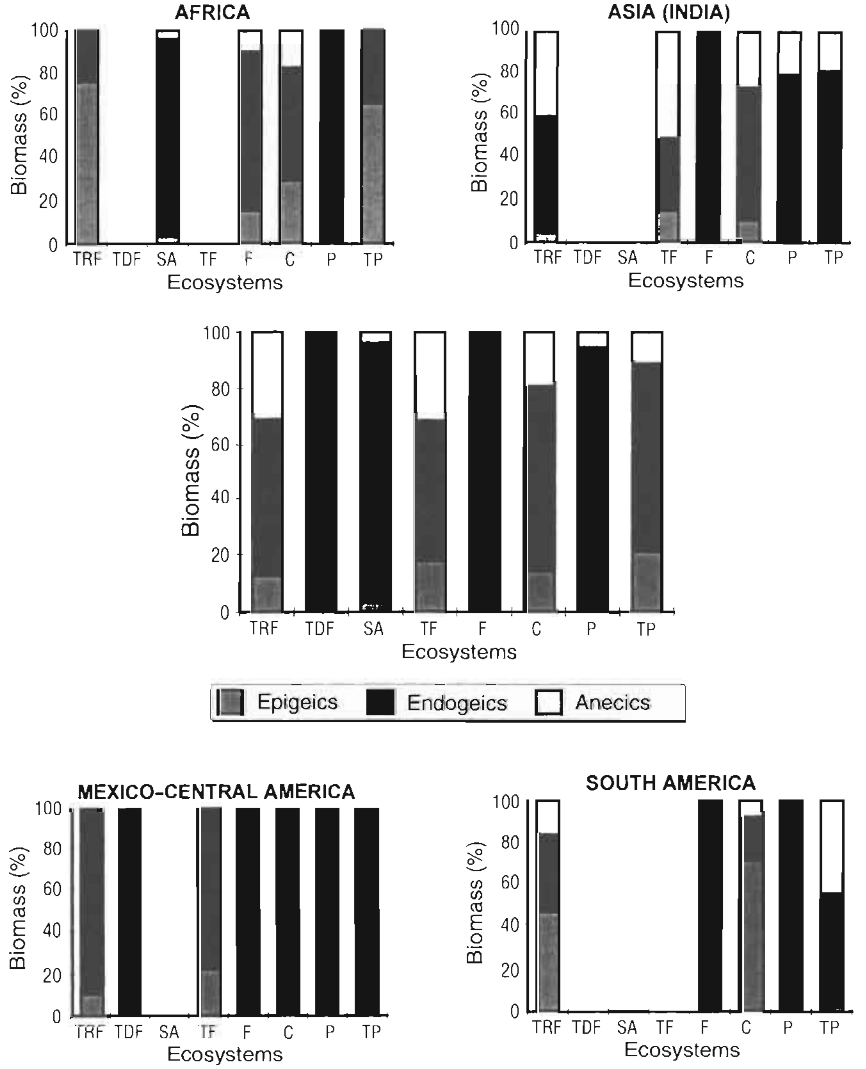

Fig. 2.8. Average functional structure (central graphic) of earthworm communities from natural (TRF, TDF, SA, TF) and managed ecosystems (F, C, P, TP) of the humid tropics. The lateral graphs show average structures according to geographical region (C = crops, F = fallows, P = pastures, SA = savannas, TDF = tropical subdeciduous forests, TF = temperate forests, TRF = tropical rainforests, TP = tree plantations).

kind of agroecosystem. This is clearly illustrated when the percentage of biomass of the main ecological categories is analysed in relation to land-use system and geographical region (Fig. 2.8); accordingly, the following patterns can be recognized:

1. There is a trend towards an endogeic domination in agroecosystems, although this is greatly influenced by the nature of the original community. Thus, in India and South America, anecic species are present in the majority of agroecosystems because they were already common in natural forests; in Mexico–Central America, on the other hand, anecic and epigeic species are totally absent in agroecosystems because these groups are absent or relatively uncommon in the natural forests.
2. If a structurally diverse community exists in natural forests, tree plantations will resemble it more than that in any other land-use system.
3. The structure of pasture communities tends to be dominated by endogeics more than in any other type of land-use system.

Changes in the structure of communities are also produced by the invasion of exotic species, a variable closely linked to the history of parcels and type of agricultural practices. Therefore, one way to make an indirect evaluation of the intensity of disturbance is by comparing the percentage of biomass contributed by native and exotic species in different agroecosystems. From comparisons shown in Fig. 2.9, the following general patterns are observed:

1. In crop and tree plantations, exotic earthworms comprise between 20 and 30% of total biomass; this trend, however, is markedly different between the four regions: in Africa this group is almost non-existent (at least in the cultivated fields of Ivory Coast and Congo), whereas in the other regions their presence is more important, increasingly from Asia (30–50%) to Central America and South America (40–60%).
2. In pastures, exotics are better represented in Mexico–Central America and South America (60–70%) than in Africa (47%) and India (8%). In the first case, the biomass of exotics was far higher than the corresponding value of natives, although recent studies in pastures from Central Veracruz, Mexico, suggest that native species could be more important (Ortiz and Fragoso, unpublished data). This regional difference also applies when we consider absolute values of total density and biomass: in agroecosystems from Africa and India, native earthworms have higher values than in the other two regions.

These results suggest three possibilities: (i) in Mexico, Central America and South America, exotic earthworms have been introduced more often and/or have found fewer restrictions to their dispersal than in African–Indian regions; (ii) agroecosystem practices in Africa and India have been more favourable for survival of native earthworms than in the other regions; and (iii) both (i) and (ii).

The influence of agroecosystem practices

In this section, we will try to determine the extent to which the survival of native species and/or the invasion of exotic species is related to management practices. In this regard, we should try to clarify whether the former African

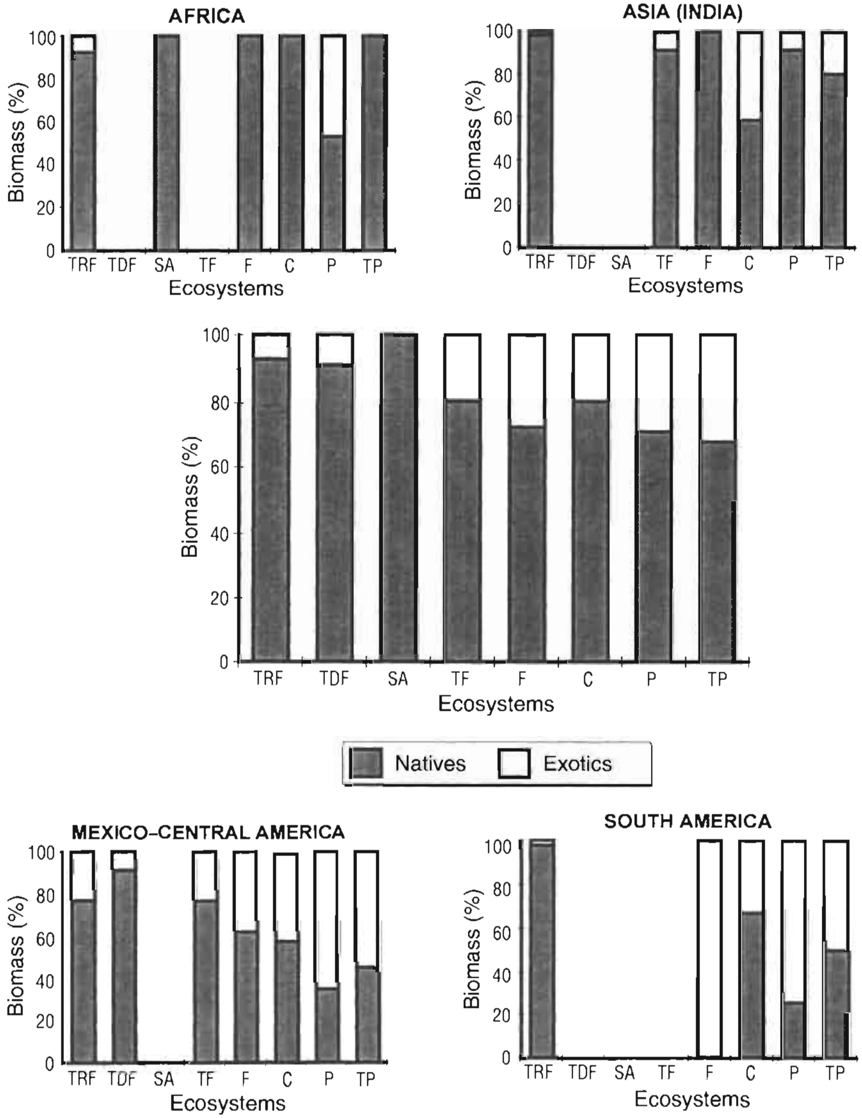

Fig. 2.9. Average relative biomass of exotic and native earthworm species in natural (TRF, TDF, SA, TF) and managed ecosystems (F, C, P, TP) of the humid tropics. The lateral graphs show average values in different geographical regions. (C = crops, F = fallows, P = pastures, SA = savannas, TDF = tropical subdeciduous forests, TF = temperate forests, TRF = tropical rain forests, TP = tree plantations).

and Indian pattern is due to different management practices. Figure 2.10 shows the relative abundance of exotic and native earthworm species in sites with different types of agricultural practices (low vs. high input) and ages of

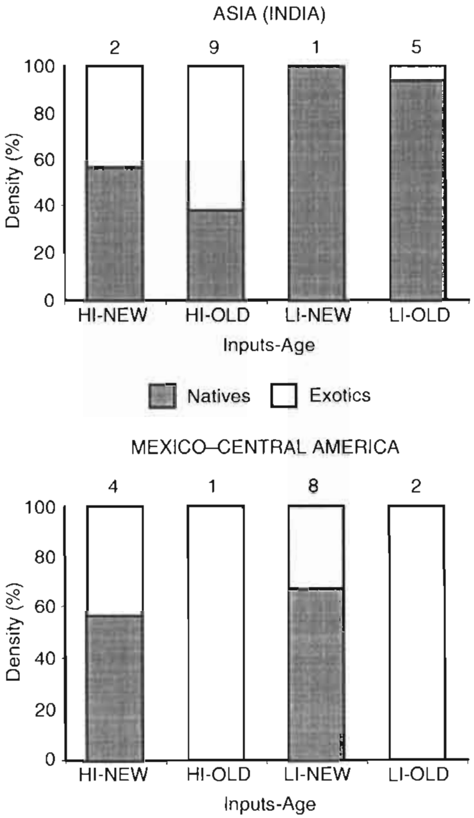

Fig. 2.10. Relative abundance of exotic and native earthworm species in agroecosystems of India and Mexico–Central America, with different intensities of agricultural practices (HI = high input, LI = low input) and ages of disturbance (NEW, OLD). Values above the bars indicate the number of sites.

perturbation (recent vs. old). Due to the small number of sites from which this information was available, Fig. 2.10 only compares the regions of Asia (India) and Mexico–Central America. Notwithstanding that in both regions the abundance of exotics was influenced positively by the intensity of agricultural practices (the average percentage over the two regions for exotic abundance in high- and low-input systems was 62 and 34%, respectively), the main conclusion of this figure is that in India native species are more resistant to disturbance than in Mexico, and/or in Mexico exotic species have been introduced more frequently. Due to the scarce information obtained about the history and management practices in parcels, these conclusions must be drawn with caution.

Conclusions

In this study the fundamental question posed was what are the parameters controlling the structure and composition of earthworm communities in tropical agroecosystems? The results presented in this chapter show that earthworm communities of tropical agroecosystems are modified both at the taxonomical and functional level, due to the action of a suite of three hierarchically related factors.

1. The geographic–phylogenetic component, followed by the influence of soils, is important in determining the functional structure of the community (i.e. ecological categories). For example, the agroecosystem earthworm communities found in Africa and South America and those derived from nutrient-poor and very humid forests found elsewhere, will differ considerably from the original ones (shift from epigeic- to endogeic-dominated communities).
2. Parcel history and local agricultural practices are largely responsible for biodiversity differences (i.e. dominance of native species in India and Africa versus dominance of exotic species in America). Other variables include the available pool of exotic invaders, dispersal rates of invading species, time elapsed since perturbation, etc.
3. Diversity of communities and overall abundance of earthworms is also influenced by the type of agroecosystem. For example, annual crop sites (independently of the geographical region) have the poorest communities, in terms of both abundance and ecological categories.

All the communities analysed in this study were assembled spontaneously, without any human participation. The challenge for the future will be to manipulate these communities in order to assess and optimize the impact of different assemblages on soil fertility and crop production.

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3

Ecology of Earthworm Species with Large Environmental Tolerance and/or Extended Distributions

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Summary

Ecological and demographic parameters of 26 species of native and exotic earthworm species common in tropical agroecosystems, with large environmental tolerance and/or extended distribution were investigated. Principal component analysis (PCA) isolated four groups: (i) large native endogeic and anecic species (16–32 g individual fresh wt) with long generation time (2–4 years), low fecundity (0.5–3.1 cocoons year^{-1} adult^{-1}) and one hatchling per cocoon; (ii) medium size species (1.2–6 g) endogeic mesohumic, with intermediate fecundity (1.3–45 cocoons year^{-1} adult^{-1}); (iii) small species (0.17–1.25 g f.w.) mainly endogeic polyhumic, with short generation time (3–7 months), intermediate fecundity (10–68 cocoons year^{-1} adult^{-1}) and one hatchling per

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cocoon; and (iv) generally small (80–550mg f.w.) species mainly exotic and epigeic, with short generation time (1–3 months), very high fecundity (50–350 cocoons year^{-1} adult^{-1}) and up to three hatchlings per cocoon.

Casts may be either large globular or small granular. The selective ingestion of large organic particles and small mineral particles (clays) concentrates total organic matter in the casts. There is an intense mineralization rate of nitrogen in the casts (6–29% of organic N), exotic worms seeming to be less efficient than natives at mineralizing N. The mineral phosphorus content of casts is always at least 30% higher than in the non-ingested soil. All these worms ingest daily, on average, three times their own weight of soil at the adult stage (1–9) and much more when juvenile; up to 1000 Mg dry soil ha^{-1} may transit yearly through earthworm guts.

Introduction

A preliminary list of 44 native and exotic earthworm species common in tropical agroecosystems has been compiled. They are able to resist disturbances linked to agricultural and agroforestry practices and build up sizeable populations in these environments (see Fragoso *et al.*, Chapters 1 and 2). However, among this group, only 10–12 may survive in annual cropping systems and maintain large populations. Up to now, basic ecological parameters of only 50% of the species of this list have been analysed to evaluate:

1. Their ability to colonize new environments, mainly based on *demographic parameters* since active dispersal (migration) is highly limited in earthworms.
2. Patterns of their *spatial distributions*, especially in changing environments.
3. Their *short-term effects on soil structure* via the selective ingestion of mineral and organic particle size fractions and the production of casts of a given structure.
4. Short-term effects on *mineralization of N and transformations of P* in casts.

The ecological parameters were taken from the literature or measured in our programme. Most data were obtained in laboratory cultures using a set of standard methods (Lavelle, 1978). The set of 26 species (Table 3.1) includes 19 recommended by Fragoso *et al.* (Chapter 1) and seven others that are or were studied because of their presence at specific sites, such as Lamto, Ivory Coast and Carimagua, Colombia.

The catalogue of species comprises five epigeics, four anecics or epianecics, and 17 endogeics, including seven polyhumics, four endoanecics (deep-dwelling endogeics that feed in the upper soil horizon), two mesohumics and two oligohumics. Table 3.1 lists the major characteristics of these groups.

Considerable numbers of species, mainly natives, did not grow in laboratory conditions. This was the case, for example, for *Rhinodrilus pashanasi* (Yurimaguas, Peru) or *Zapatadrilus* sp. nov.1 (Panuco, Mexico) and *Martiodrilus carimaguensis* (Carimagua, Colombia), although they are

Table 3.1. Classification of earthworms into ecological categories (after Bouché, 1977; Lavelle, 1981; Fragoso and Lavelle, 1987).

Categories	Sub-categories	Habitat	Food	Size and pigmentation
Epigeics	Epigeic	Litter	Leaf litter	<10 cm, highly pigmented
	Epianecic	Surface soil	Leaf litter	10–15 cm, partly pigmented
Anecics	Anecic	Live in burrows	Litter + soil	>15 cm, anterodorsal pigmentation
Endogeics	Polyhumic	Surface soil or rhizosphere	Soil with high organic content	<15 cm, filiform, unpigmented
	Mesohumic	Upper 0–20 cm	Soil from the 0–10 cm strata	10-20 cm, unpigmented
	Endoanecic	0–50 cm, some dig burrows	Soil from the 0–10 cm strata	>20 cm, unpigmented
	Oligohumic	15–80 cm	Soil from 20–40 cm strata	>20 cm, unpigmented

important native species in some moderately disturbed agroecosystems. This reflected their inability to be produced in massive cultures for inoculation. Any manipulation of these populations has to be indirect. The measured demographic parameters were fecundity, generation time, time of incubation of cocoons and the identification of the type of reproduction (parthenogenetic vs. amphimictic). Other relevant ecological parameters were size (length and width at the adult stage) and ingestion rates (Table 3.2).

Demographic Parameters

Among these 26 species, eight are exotics with worldwide distributions (*Eudrilus eugeniae, Pontoscolex corethrurus, Polypheretina elongata, Metaphire posthuma, Ocnerodrilus occidentalis, Dichogaster bolaui, Perionyx excavatus* and *Eisenia andrei*); 18 are native, six are euryecic species with a wide regional distribution (*Bahanteodrilus pearsei, Hyperiodrilus africanus, Eminoscolex lavellei, Onychochaeta elegans, Chuniodrilus zielae* and *Dichogaster agilis*) and the other 13 are stenoecic natives of different origins (Table 3.2).

A principal component analysis (PCA; Anamul programme for Macintosh) of this data set (Table 3.2) was performed, and the missing values were standardized in order to make all biological factors equally important. This analysis allowed the identification of two major significant components that explained 40 and 17.2% of variance respectively (Fig. 3.1). Axe I characterizes the relationship between adult size and demographic parameters; axe II indicated an inverse relationship between the average depth at which

Table 3.2a. Ecological and biological parameters of selected tropical earthworm species.

									Adult				Ingestion rate		
					Origin								Adult	Juvenile	
Species	Reference	Native or exotic	Steno or eury	Ecological category	Country	Site	Soil type	Generation time (months)	Weight (gf.w)	Length (mm)	Width (mm)	L/W	g dry weight g^{-1}	Ew day^{-1}	Cast shape
Agastrodrilus opisthogynus	Omodeo and Vaillaud, 1967	Native	Steno	Polyhumic	Ivory Coast	Lamto	Alfisol	24	3	300	5	60	–	–	Granular
Diplotrema papillata	James, 1990	Native	Steno	Polyhumic	Mexico	Palma Sola	Vertisol	4.5	0.23	34	2	23	3.25	–	Granular sticks
Millsonia anomala	Omodeo, 1954	Native	Steno	Mesohumic	Ivory Coast	Lamto	Alfisol	20	4.5	170	6	28	6	2	Large globular
Andiodrilus yoparensis	Jimenez and Moreno, in preparation	Native	Steno	Mesohumic	Colombia	Carimagua	Oxisol	12	1.34	109	4	25	2.25	4.3	Large globular
Dichogaster l. nigrae	Saussey, 1966	Native	Steno	Oligohumic	Ivory Coast	Lamto	Alfisol	36	29	300	7.5	40	3.5	8	Large globular
Millsonia ghanensis	Sims, 1965	Native	Steno	Oligohumic	Ivory Coast	Lamto	Alfisol	42	16	300	9	33	5	12	Large globular
Martiodrilus carimaguensis	Jimenez and Moreno in preparation	Native	Steno	Anecic	Colombia	Carimagua	Oxisol	24	11.24	194	9	21	0.85	3	Large globular
Millsonia lamtoiana	Omodeo and Vaillaud, 1967	Native	Steno	Anecic	Ivory Coast	Lamto	Alfisol	24	32	450	10	45	0.61	–	Large globular
Drawida willsi	Michaelsen, 1907	Native	Steno	Epianecic	India	Sambalpur (paddy)	Sandy loam	4	0.15	54	2	30	6.5	–	Small globular
Glossoscolecidae sp.	Fragoso, in preparation	Native	Steno	Endoanecic	Mexico	La Vibora	Inceptisol	4.2	0.53	120	3	48	4.05	1.5	Small granular
Chuniodrilus zielae	Omodeo, 1963	Native	Eury	Polyhumic	Ivory Coast	Lamto	Alfisol	18	0.2	70	2	35	4.5	15	Fine granular
Dichogaster agilis	Omodeo and Vaillaud, 1967	Native	Eury	Epigeic	Ivory Coast	Lamto	Alfisol	15	0.5	70	4	16	4.2	–	Med. granular vg debris
Hyperiodrilus africanus	Beddard, 1893	Native	Eury	Epiendogeic	Ivory Coast	Lamto	Alfisol	1.9	0.72	160	4	40	9	20	Granular
Protozapotecia australis	James, 1993	Native	Eury	Polyhumic	Mexico	Laguna Verde	Vertisol	3	0.48	120	2	60	1.5	1.6	Small granular
Eminoscolex lavellei	Kanyonyo and Omodeo, in preparation	Native	Eury	Polyhumic	Rwanda	Butare		4	0.35	66.5	4	26	4	15	Small granular
Balanteodrilus pearsei	Pickford, 1938	Native	Eury	Polyhumic	Mexico	La Mancha	Psamment	4.5	0.17	38	2	25	1.02	–	Small granular
Onychochaeta elegans	Cognetti, 1905	Native	Eury	Mesohumic	Cuba	La Habana	Luvic phaeozem	3.5	0.85	80	5	16	0.26	0.8	Large globular
Lampito mauritii	Kinberg, 1867	Native	Eury	Anecic	India	Sambalpur (grassland)	Loam	7.7	1.22	145	4	36	2.25	–	Globular granular
Ocnerodrilus occidentalis	Eisen, 1878	Exotic	Eury	Polyhumic	India	Sambalpur (paddy)	Sandy loam	2.5	0.04	80	2	53	–	–	Small globular
Pontoscolex corethrurus	Muller, 1856	Exotic	Eury	Mesohumic	India	Valparai (tea)	Laterite	4	1.25	90	5	18	1.25	–	Globular
Pontoscolex corethrurus		Exotic	Eury	Mesohumic	Mexico	La Vibora	Inceptisol	3.8	0.85	50	4	13	3.15	2.2	Large globular
Pontoscolex corethrurus		Exotic	Eury	Mesohumic	Mexico	Laguna Verde	Vertisol	3.5	0.6	50	4	13	2	4.3	Large globular
Polypheretima elongata	Perrier, 1872	Exotic	Eury	Mesohumic	India	Sambalpur (orchard)	Loam	8.5	3.3	192	5	43	1.5	–	Large globular
Polypheretima elongata		Exotic	Eury	Mesohumic	Martinique	St. Anne	Vertisol	4.5	6	200	8	25	1	10	Large globular
Metaphire posthuma	Vaillant, 1868	Exotic	Steno	Endoanecic	India	Delhi (garden)	Sandy clay	7	1	100	5	10	–	–	Granular
Dichogaster bolaui	Michaelsen, 1891	Exotic	Eury	Epigeic	India	Sambalpur (garden)	Loam	3	0.08	331	2	21	–	–	Fine globular
Eudrilus eugeniae	Kinberg, 1867	Exotic	Eury	Epigeic	South Africa		Cow manure	2	3.12	175	6	29	–	–	Small granular sticks
Eisenia andrei	Bouché, 1972	Exotic	Eury	Epigeic	Mexico	Xalapa	Coffee pulp	1.5	0.73	105	4	24	0.14	0.3	Small granular sticks
Perionyx excavatus	Perrier, 1872	Exotic	Eury	Epigeic	Mexico	Xalapa	Coffee pulp	1.2	0.55	80	5	16	0.1	0.3	Small granular sticks

Table 3.2b.

Species	Fecundity cocoons/ adult/year F	Cocoons			Hatchling weight (mg)	Adult weight/ cocoon weight	Reprod. amphi. or partheno.	Mean distribution depth (cm)	Pigment[a]	Resistance form	Ability to be cultured	Reference
		Weight (mg)	Incubation time (days)	No. ind. /cocoon								
Agastrodrilus opisthogynus	1.3	121	35	1	–	25	s	29	0	Quiescence	0	Lavelle (1978)
Diplotrema papillata	36	5	15	–	–	45		5	+	Diapause	••	Barois *et al.*[b]
Millsonia anomala	7.5	50	23	1	–	90	s	8	0	Quiescence		Lavelle (1978)
Andiodrilus yoparensis	1.7	79	28	1	55	17	s	9	0	Quiescence	•••	Jimenez and Moreno[b]
Dichogaster t. nigrae	1.9	315	22	1	130	92	s	23	0	Quiescence	••	Lavelle (1978)
Millsonia ghanensis	1.3	200	36	1	–	80		32	0	Quiescence		Lavelle (1978)
Martiodrilus carimaguensis	0.5	1808	48	2	760	6.2	s	35	++	Diapause	••	Jimenez and Moreno[b]
Millsonia lamtoiana	3.1	320	31.5	1	–	100		7	+++	Quiescence		Lavelle (1978)
Drawida willsi	14.5	14	14	2.5	6.5	11		5	++	Diapause	••	Sahu (1988), Senapati *et al.*[c]
Glossoscolecidae sp.	10.8	35.2	40	1	27	15	p/s?	10	++	Quiescence	••	Barois *et al.*[b]
Chuniodrilus zielae	13	2.2	26.5	1	1.8	93	s	18	0	Quiescence	••	Lavelle (1978)
Dichogaster agilis	10.7	9	26.5	1		56	s	6	+++	Quiescence	••	Lavelle (1978)
Hyperiodrilus africanus	109.5	20	15	2	2.1	36	p	5	+	Quiescence		Tondoh (1994)
Protozapotecia australis	10.1	7.5	–	1	–	63		5	++	Quiescence	••	Barois *et al.*[b]
Eminoscolex lavellei	51	–	–	–	4.8			10	+	Quiescence	••	Kanyonyo[b]
Balanteodrilus pearsei	25	4	20	1	2.8	42	s	10	0	Quiescence	••	Fragoso and Angeles[b]
Onychochaeta elegans	6.5	43	18	1	40	23	s	10	0	Quiescence	••	Martinez[b]
Lampito mauritii	11.8	61	28	1.5	24	20	s	10	++	Quiescence	••	Dash and Senapati (1980)
Ocnerodrilus occidentalis	25	–	–	–	–		p/s	8	0	Diapause	••	Sahu (1988), Senapati *et al.*[c]
Pontoscolex corethrurus	27	28.5	39.5	1	25	44	p	13	0	Diapause	••	Senapati *et al*[c]
Pontoscolex corethrurus	25	38.6	34	1	26.3	22	p	10	0	Quiescence	••	Barois *et al.*[b]
Pontoscolex corethrurus	67.5	38.5	40	1	27	16	p	10	0	Quiescence	••	Lavelle *et al* (1987)
Polypheretima elongata	19.1	73.5	28	1	45	45	p	30	0	Migration in depth	••	Sahu (1988), Senapati *et al.*[c]
Polypheretima elongata	45	38.2	51.5	1.2	27.5	157	p	25	0	Migration in depth	••	Lavelle[b]
Metaphire posthuma	10	58	29	1	–	17	s	10	0	Quiescence	••	Senapati *et al*[c]
Dichogaster bolaui	46.6	6.5	8.5	2	2.5	12	s	5	+++	Cocoon	••	Sahu (1988), Senapati *et al.*[c]
Eudrilus eugeniae	347	17	16.6	2.7	6.2	183	s	0	+++	Cocoon	•••	Viljoen and Reinecke (1989)
Eisenia andrei	52.1	19	18.5	3	6.5	38	s	0	+++	Cocoon	•••	Barois *et al.*[b]
Perionyx excavatus	365	23	18.5	2	4.6	24	p/s	0	+++	Cocoon	•••	Barois *et al.*[b]

[a] Pigmentation: 0 = none; + anterior, ++, antero-dorsal; +++ whole body. [b] Unpublished data. [c] Data from Senapati (1980) or Senapati and Sahu (1993 a,b) and Senapati *et al.* (1993, 1995, unpublished data)

populations live and fecundity number of hatchlings per cocoon, respectively. A cluster analysis allowed separation of four major groups of species (Fig. 3.2):

1. Group 1 comprises large endogeic and anecic native species (12–32 g fresh wt) with a long generation time of 2–4 years, low fecundity (0.5–3.1 cocoons year^{-1} adult^{-1}) and only one hatchling per cocoon.
2. Group 2 is rather heterogeneous and comprises medium size species (1.2–6 g), with fecundity of 1.3–45, and generally one hatchling per cocoon except for *P. elongata* (1.2).
3. Group 3 contains a large number of endogeic species of relatively small size (170–1250 mg), with generation time of 3–7 months for most species, except *D. agilis* (15 months) and *C. zielae* (18 months), intermediate fecundity of 10–25 cocoons adult^{-1} year^{-1}, except for *P. corethrurus* (up to 68), *E. lavellei*

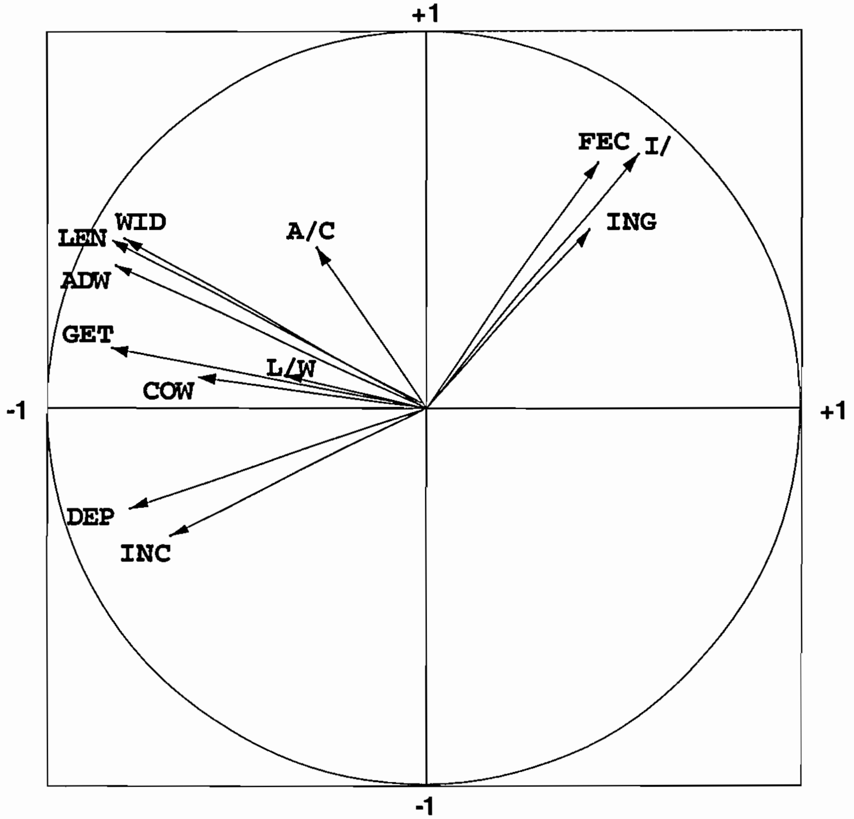

Fig. 3.1. Correlations between principal components and morphological and demographic parameters of 26 native and exotic earthworm species of the humid tropics. A/C = ratio of adult to cocoon weight, ADW = adult weight, COW = cocoon weight, DEP = depth, FEC = fecundity, GET = generation time, I/ = number of hatchlings per cocoon, INC = time of incubation, ING = ingestion rate, LEN = length, L/W = length to width ratio, WID = width.

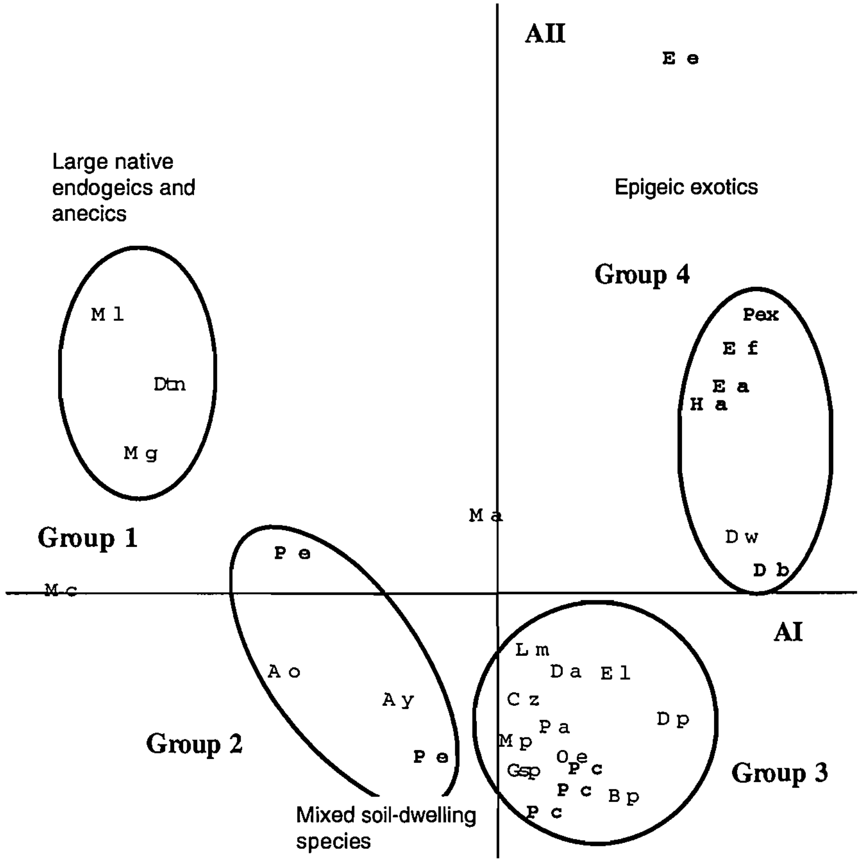

Fig. 3.2. Relative positions of species along axes I and II. (Ao = *Agastrodrilus opisthogynus*, Ay = *Andiodrilus yoparensis*, Bp = *Balanteodrilus pearsei*, Cz = *Chuniodrilus zilae*, Da = *Dichogaster agilis*, Db = *Dichogaster bolaui*, Dp = *Diplotrema papillata*, Dt = *Dichogaster terrae-nigrae*, Dw = *Drawida willsi*, Ea = *Eisenia andrei*, Ee = *Eudrilus eugeniae*, Ef = *Eisenia fétida*, El = *Eminoscolex lavellei*, Gsp = Glossoscolecidae sp, Ha = *Hyperiodrilus africanus*, Lm = *Lampito mauritii*, Ma = *Millsonia anomala*, Mc = *Martiodrilus carimaguensis*, Mg = *Millsonia ghanensis*, Ml = *Millsonia lamtoiana*, Mp = *Methaphire posthuma*, Oe = *Onychochaeta elegans*, Oo = *Ocnerodrilus occidentalis*, Pa = *Protozapotecia australis*, Pc = *Pontoscolex corethrurus*, Pe: *Polypheretima elongata*, Pex = *Perionyx excavatus*. Exotics are indicated in bold.

(51) and *Diplotrema papillata* (36), and one hatchling per cocoon except for *Lampito mauritii* (1.5).

4. Group 4 is the opposite to group 1; it contains six species that are mainly exotic epigeic, four of them being used for vermicomposting. These species are generally small (80–550 mg) have short generation times (1–3 months), high

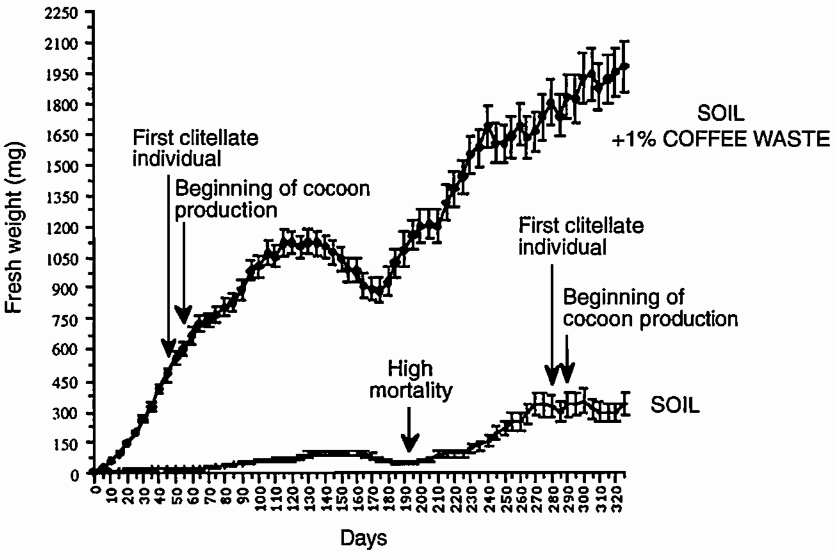

Fig. 3.3. Growth of *Hyperiodrilus africanus* in control soil and soil enriched with 1% coffee waste (Tondoh, 1994).

fecundity (50–350 cocoons adult^{-1} year^{-1}) and up to three hatchlings per cocoon.

Three species stand outside the clusters, *Martiodrilus carimaguensis* a large species of the Colombian llanos, close to group 1 and producing remarkably large cocoons (1.8 g fresh wt, i.e. 16% of adult weight) that yield two individuals on average; *Millsonia anomala*, a relatively large species that lives close to the soil surface (8 cm depth on average); and *Eudrilus eugeniae*, a large epigeic species used for vermicomposting.

In a given group, exotic species tend to have higher fecundity and shorter generation time than native species. Most species of group 4 ('vermicomposting' species) are exotics, whereas group 1 (large long-living endogeics and anecics) only contains natives.

A few apparently important parameters do not discriminate among species. They are length to width ratio (L/W) which varies from 13 to 60; ingestion rate of adults (0.5–9.1 g dry wt g^{-1} fresh wt of worm); incubation time of cocoons (9–52 days) and the ratio of adult to cocoon weight (11–184). Cocoons of exotic species, for instance, may be either small (*P. elongata* and *E. eugeniae* with respective A/C ratios of 245 and 184) or large (*D. bolaui* and *P. corethrurus* with respective values of 12 and 16).

In field conditions, demographic parameters may vary considerably depending on soil moisture and organic content. At Lamto (Ivory Coast), for instance, *H. africanus* can only grow if the soil of the upper 10 cm is supplemented with organic residues. Growth and fecundity then depend on soil moisture and the quality of the residue (Fig. 3.3, Tondoh, 1994) or the soil organic

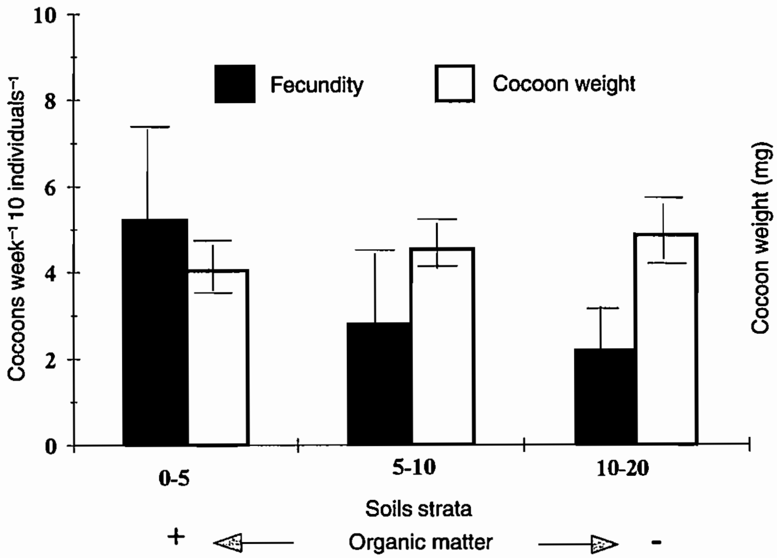

Fig. 3.4. Fecundity and cocoon weight of *Balanteodrilus pearsei* from La Mancha (Mexico) grown in three soil strata (from Angeles, 1996).

matter. *Balanteodrilus pearsei*, the most widely distributed native species in southeastern Mexico, found in disturbed and undisturbed sites, was grown in a soil of La Mancha from the strata 0–5, 5–10 and 10–20 cm, having a C content of 2.46, 1.76 and 1.06%, respectively; its fecundity was highest in the richest layer but the weight of the cocoons was smallest (Fig. 3.4). This physiological trend may be related to a resource allocation strategy involving an energy reproduction threshold: the more adverse the environment, the fewer cocoons are produced but their weight is larger in order to give them a greater chance of survival (Angeles Varela, 1996; Fragoso and Angeles, unpublished).

Temperature may also have some effect in mountain regions. *P. corethrurus*, for example, can only reproduce at temperatures above 23°C (Lavelle *et al.*, 1987), and growth is twice as fast at 25 than at 20°C. Hamoui (1991) determined a generation time for *P. corethrurus* of 19 months in the region of São Paolo, Brazil, where the mean annual temperature is 22°C, while in the warmest regions of Mexico and India it is 4 months.

Therefore, technologies using these earthworms will be limited to regions with temperatures above 20°C and annual rainfall >1000–1200 mm. More generally speaking, the availability of organic matter or residues to feed the worms is often a major limitation to earthworm activities in agroecosystems where organic stocks may be highly depleted. For example, growth of *P. elongata* at St Anne (Martinique) is highly limited in soils subjected to intensive market gardening (Blanchart, 1997); in that case, a dramatic decrease in

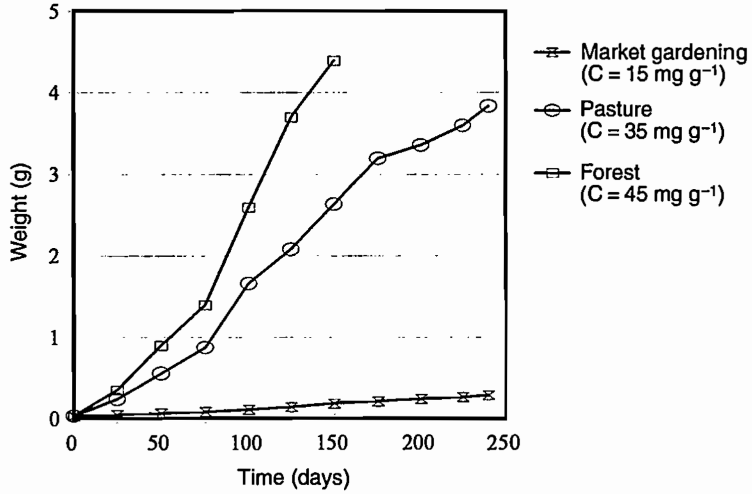

Fig. 3.5. Comparative growth of *Poypheretima elongata* in Vertisols with different C contents (Blanchart *et al.*, unpublished data).

SOM content of cropped soils explains the disappearance of earthworm populations (Fig. 3.5; see Chapter 4).

Spatial Distribution Patterns

The horizontal distribution patterns have been analysed by Taylor's power law index of aggregation (Taylor, 1961, 1971). Geostatistical analysis (Robertson, 1987; Rossi *et al.*, 1995) was used to map earthworm density patterns across the field plots.

The measure of spatial distribution by Taylor's index shows that most earthworm species exhibit aggregated spatial distributions. The index was found to be highly correlated with the demographic and morphological variables and particularly with fecundity and size. Species with high fecundity and small size are highly aggregated. On the contrary, large species with low fecundity display spatial distributions close to random (i.e. *b* values close to 1, Table 3.3). In general, the maps of earthworm density reveal diversity of the aggregation patterns. However, a clumped nature of earthworm distribution corresponds to the presence of large patches, 10–30 m in diameter that are often observed in various ecosystems and for different species (Rossi *et al.*, 1995, 1997; Rossi and Lavelle, 1996). An example is given in Fig. 3.6 for *Glossodrilus sikuania* n.sp. density from the oriental llanos of Carimagua, Colombia. The map reveals the presence of two large patches in a 70 × 70 m plot (J.J. Jimenéz, unpublished data).

Table 3.3. Aggregation index (Taylor's power law) for a range of tropical earthworm species. Exotics are indicated in bold.

Species	Taylor's index *b* values	Standard error
Agastrodrilus opisthogynus	1.140	0.13
Millsonia anomala	1.626	0.221
Dichogaster terrae nigrae	1.121	0.069
Millsonia ghanensis	1.025	0.076
Millsonia lamtoiana	1.026	0.007
Chuniodrilus zielae	1.724	0.169
Dichogaster agilis	1.324	0.084
Balanteodrilus pearsei	1.3	0.1
Onychochaeta elegans	2.12	0.08
Ocnerodrilus occidentalis	1.22	0.2
Pontoscolex corethrurus	1.63	0.11
Polypheretima elongata	1.87	0.12

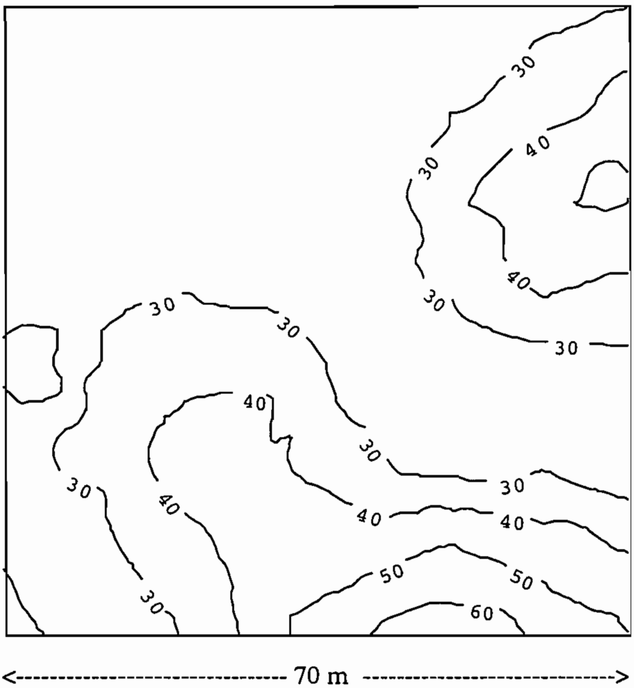

Fig. 3.6. Horizontal distribution of small polyhumic *Glossodrilus sikuania* in *Brachiaria decumbens* + *Pueraria phaseoloides* pasture at Carimagua (Colombia) in the Oriental llanos (November, 1994) in a 70 × 70m square plot. Contours represent earthworm density (ind m^{-2}).

Soil Ingestion Rates and Particle Size Selection

Ingestion rates

Ingestion rates are highly variable. They change with feeding habits, temperature and moisture conditions, the size and physiological state of individuals, and also among species. In optimal conditions, native African species may ingest several times their own weight of soil daily. Maximum values of 25–30 g of dry soil g^{-1} fresh wt day^{-1} have been measured in young *M. anomala*. Most values are in the range of 1–10 g daily. In proportion, larger worms eat less than small worms and adults ingest lower amounts of soil than juveniles (Tondoh, 1994; Fig. 3.7).

Species that ingest litter mixed with soil tend to have lower ingestion rates. Within a single population, individuals tend to ingest less substrate when fed on a richer soil (Lavelle *et al.*, 1989). For example, adults of *H. africanus* when fed soil with 1% litter of *Chromolaena odorata* ingest on average 6 g EW g^{-1} fresh wt day^{-1}, i.e. threefold their ingestion rate when fed the same soil supplemented with 1% coffee waste (Fig. 3.7).

Extrapolation of these data at the level of a whole community provides figures of several hundred megagrams of dry soil ha^{-1} $year^{-1}$ ingested in systems with earthworm biomasses of 300–1000 kg fresh wt. At Lamto (Ivory Coast), detailed estimates gave figures of 600–1200 Mg ha^{-1} $year^{-1}$ depending on the type of savanna and rainfall (Lavelle, 1978).

However, the comparison of ingestion rates among species having different feeding habits is difficult. When the ingested substrate is soil, the volume

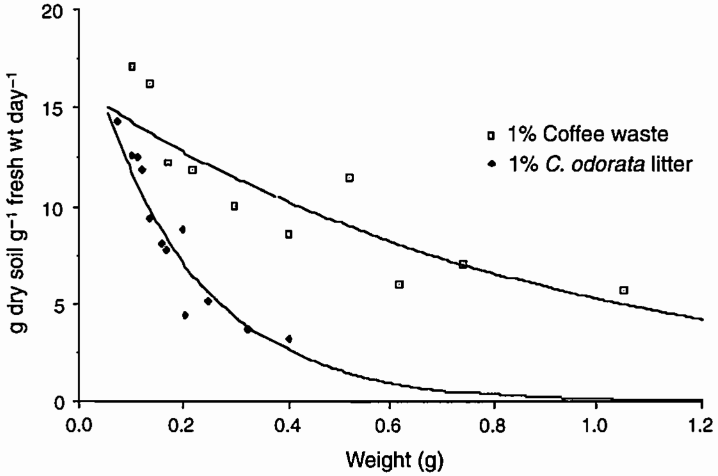

Fig. 3.7. Soil ingestion rate of *Hyperiodrilus africanus* as a function of individual weight in soil enriched with 1% litter of *Chromolaena odorata* and 1% coffee waste (Tondoh, 1994).

and weight of the dry ingested material are not dramatically different from the fresh material. Conversely, when they feed on litter, the ingestion rate expressed in dry weight is very different from that in fresh weight. For example, the coffee pulp is 80% water and 20% dry matter; the epigeic *E. andrei* and *P. excavatus* fed on this substrate have an ingestion rate of 0.1 g dry wt or 5 g fresh wt EW g^{-1} day^{-1}.

Cast shape

Endogeic earthworms, except the oligohumic species, deposit part of their castings on the soil surface. The shapes of the casts are mainly of two types: large globular or small granular. The first can be produced as towers or small mounds and the second is scattered when deposited at the soil surface. In soil, both types can fill galleries and burrows. The deposition of casts on the soil surface is relevant for erosion (Shipitalo and Protz, 1989). Fresh casts have very low structural stability, on the other hand dry casts are highly water-stable after their external surface has solidified, forming a cortex which results from the arrangement of clays and organic materials such as polysaccharides (Blanchart, 1990; Blanchart *et al.*, 1993; see Chapter 5). The size and shape of casts are important for soil structure and porosity; the large globular casts are compact structures (the size of the casts of *M. carimaguensis* is 10 cm × 5 cm), the accumulation of which can lead to decreases in soil porosity and water infiltration, while the small granular casts generally favour the decompaction of soil (Blanchart *et al.*, 1997). In both cases, the increase in organic matter will influence these characteristics. The size of the earthworm is not necessarily related to the size of the casts. Large species such as *Zapatadrilus guapotus* (12 g) or *E. eugeniae* (3 g) produce small granular structures.

Selection of organic and mineral size particles

Most earthworms selectively ingest organic particles differently among ecological categories and depending on the organic content of the ingested soil (Fig. 3.8). At St Anne, for example, *P. elongata* selectively ingested large organic particles in soil from the area subjected to market gardening, and casts had a greater content of C than the control soil. In pasture, casts tended to have a lower content of coarse organic particles than the control soil (non-significant difference). However, this difference in behaviour is the result of the organic content of the soil; if the soil is poor in C, the worm acts like a polyhumic, if it is richer, it acts like a mesohumic.

Epigeics ingest mainly litter. Anecics ingest a mixture of litter and mineral soil. For example, the large African anecic *M. lamtoiana* ingests a mixture of 12% coarse organic debris and 88% soil (Kanyonyo, 1984). Guggenberger

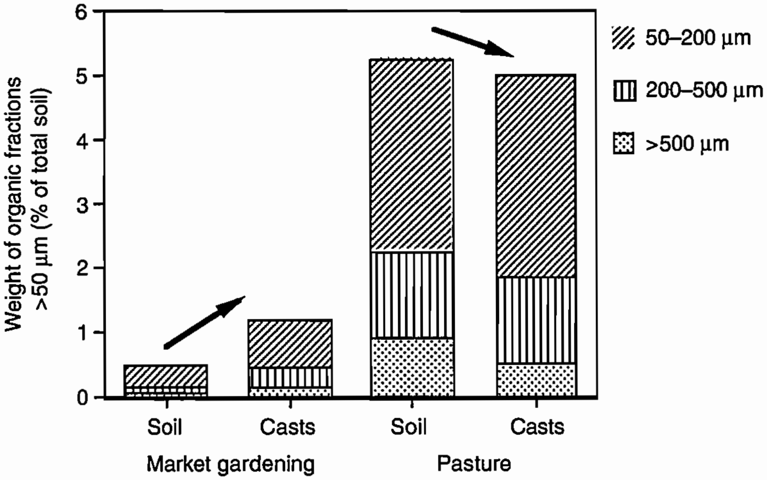

Fig. 3.8. Weight percentage of organic fractions >50 μm in casts of *Polypheretima elongata* and control vertisols from two systems in Martinique (Duboisset, 1994).

et al. (1998) showed that casts of the anecic *M. carimaguensis* had a higher proportion of plant-derived carbohydrates (hemicellulose) than bulk soil. Endogeics have different abilities to ingest organic matter selectively: oligohumics and mesohumics ingest soil of the deeper and surface (0–10) horizons, respectively, without making a significant selection of organic particles. Polyhumics select for organic particles by avoiding coarse sands and gravels and feeding in microenvironments with higher organic contents such as, for example, the rhizosphere or the upper few millimetres of soils where surface litter may have been buried under their casts, or other biological surface structures. Figure 3.9 shows in general terms, that endogeics select small aggregates and concentrate clays. However, when the soil is very clayey, e.g. for *M. carimaguensis* and *O. elegans*, sand becomes concentrated. Also, the latter can be the result of the diameter of the 'mouth' of the worm: large earthworms are able to ingest largest particles, e.g. *Z. guapotus* (12 g) and *M. carimaguensis* (12 g).

The earthworm guts acts as a 'hot spot' with intense enzyme activity for the decomposition of organic matter (Brussaard and Juma, 1996). The glucosidic enzymatic activity of the gut content of *P. corethrurus*, *P. elongata* and *M. anomala* was tested (Zhang *et al.*, 1993; Lattaud *et al.*, 1997, 1998). Results showed that these species are able to feed specifically on plant and fungal structures. Spain *et al.* (1990) previously suggested that *P. corethrurus* may derive much of its tissue C from the rhizosphere.

P. elongata from Martinique exhibited the largest number of enzymes secreted by its gut tissue. For *M. anomala* and *P. corethrurus*, the origin of most enzymes, such as cellulase and mannase, was microbial and not the gut itself. These results support the hypothesis of a mutualistic earthworm–microflora

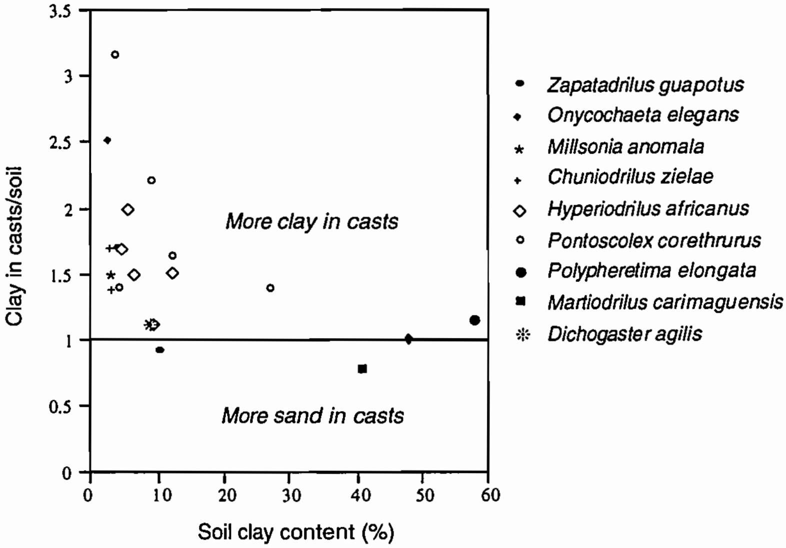

Fig. 3.9. Effects of soil clay content on selective ingestion of clay particles by different earthworm species.

digestion system for endogeic geophagous earthworms where the high production of intestinal mucus is the key process (Barois and Lavelle, 1986; Lavelle, 1986); it is the trigger of (or the priming effect for) the activation of the microflora allowing it to digest or decompose the soil organic matter.

Intestinal mucus production was measured in the anterior part of the gut of four native (Lavelle *et al.*, 1983; Martin *et al.*, 1987) and three exotic (Barois, 1992) earthworm species. Among the native species, the anecic *Millsonia lamtoiana* produced the least amount of mucus, followed by the oligohumics *Dichogaster terrae nigrae* and *Millsonia ghanensis* and the mesohumic *M. anomala* (these differences were not significant). The peregrine exotic species produced three times more intestinal mucus than the native African species (Fig. 3.10). Probably part of the success of the peregrine and exotic species is due to their capacity to have highly efficient mutualistic interactions with the soil microflora, allowing them to digest the majority of the soil organic matter.

Microorganisms, mycorrhizae and seed dispersion

Brown (1995), in his extensive review, suggested that the interactions between microorganisms and earthworms have more beneficial than negative effects. Earthworm feeding leads to a digestion, an activation and stimulation of selected microorganisms (Barois, 1987). They can also passively disperse propagules, spores and seeds.

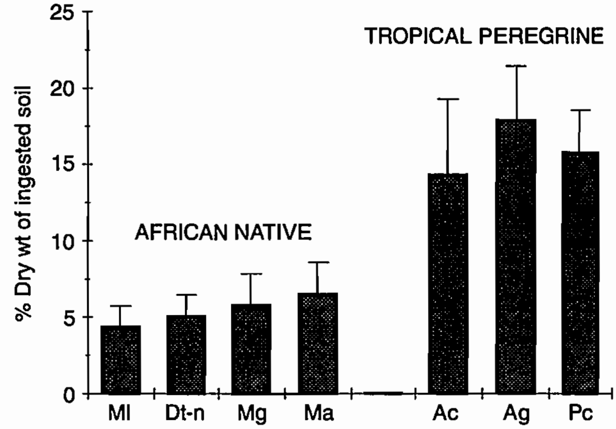

Fig. 3.10. Proportion of intestinal mucus added to the ingested soil by selected species of earthworm (after Lavelle *et al.*, 1983; Martin *et al.*, 1987; Barois, 1992). Ac = *Amynthas corticis*, Ag = *Amynthas gracilis*, Dt-n = *Dichogaster terrae-nigrae*, Ma = *Millsonia anomala*, Mg = *Millsonia ghanensis*, Ml = *Millsonia anomala*, Pc = *Pontoscolex corethrurus*.

At Yurimaguas (Peru), a pot experiment with tree seedlings of *Bixa orellana*, *Eugenia stipitata* and *Bactris gasipaes* innoculated with *P. corethrurus* showed that the earthworms highly increased the root infection by VAM as well as the N mineralization. After 180 days, the plants inoculated with 10 worms had at least three times more roots infected by VAM than the plant controls (Ydrogo, 1994). Redell and Spain (1991a,b) in tropical Australia, observed that the relative concentration of spores in casts was higher than in the general soil for *P. corethrurus* and *Diplotrema heteropora*, and that worms spread infective *Frankia* spp. (actinomycete) and spores and hyphal propagules in undigested root fragments. In air-dried casts of *E. eugeniae*, Harinikumar *et al.* (1991) also found viable VAM spores. Gange (1993) suggested that due to feeding on senescing roots, earthworms concentrate mycorrhizal propagules.

Up to now, there have been few studies done on seed dispersal by tropical earthworms although as in temperate regions they may be essential in the formation of seed banks, burying seeds and bringing them to the surface. Piearce *et al.* (1994) noted that large casts are much more effective in seed dispersal than small ones. Proportionally they contain many more seeds because their ingestion is not limited by the mouth size of the earthworm.

In Carimagua (Colombia; Decaëns, unpublished data), the soil bank seeds and the seeds excreted in the earthworms casts were measured in three ecosystems, native savanna, improved pasture and rice monocrop (Table 3.4). The ecosystem that had the highest percentage of the seed bank excreted by earthworms was the improved pasture, with 22.4%; the native savanna and rice monocrop only had 3 and 2.7%, respectively. This difference was understandable because the improved pasture had 11 times more earthworms than the

Table 3.4. Effect of the earthworm community on the seed bank and seed germination from a pasture at Carimagua (Colombia; source Decaëns).

	Earthworm density (ind m^{-2})	Soil seed bank (no. m^{-2})	Seeds excreted in casts (no. m^{-2} $year^{-1}$)	% of the seed bank excreted	% of germination in soil	% of germination in casts
Native	0.3	1526	27	3	7.5	0.8
savanna	0.5	276	6	1.1	2	0.5
Improved	3.3	13,821	2819	22.4	39	5
pasture	3.8	1228	306	4.2	3.7	0.8
Rice	0.3	15,084	367	2.7	32.5	3.3
monocrop	0.1	2445	61	0.4	5.7	0.8

others ecosystems. The earthworm population seemed not to stimulate the seed germination; in the improved pasture, the percentage of germination in casts and soil was 5 and 39%, respectively. This corroborates the observation made by Grant (1983): earthworm casts are poorly aerated and rich in ammonia, conditions known to induce seed dormancy or delay germination.

Short-term Effects on Mineralization of N and Other Nutrients and Transformations of P

Nitrogen

Significant amounts of mineral N and assimilatable P are found in fresh earthworm casts. Nitrogen is excreted as ammonium by nephridia. Some species have ectonephridia that open on the outside of the body; other species with endonephridia excrete ammonium into the gut and further into casts (Lavelle, *et al.*, 1992). Another part of mineral N originates from an enhanced microbial activity in the gut (Barois, *et al.*, 1987).

Mineral and organic N have been measured on fresh casts produced by seven different species (five natives and the two most widespread endogeics) fed on nine soils with highly different organic matter contents (Table 3.5). The percentage mineralization significantly differed among species, varying from 1.6 to 29.7%, with half of the values falling between 5 and 10%. The highest values were found in Vertisols of Martinique and a Psamment of Mexico. Lowest values were obtained in Alfisols with low N contents, and Andisols with little N in available forms from Ivory Coast. These results indicate that measurements of mineral N in casts of exotic earthworm species with broad distributions might be used to assess the pool of easily mineralizable nitrogen. In their native soils, native species promoted higher N mineralization than exotics.

Table 3.5. Total and mineral nitrogen content in soil and fresh casts from earthworms incubated in different soil types, and percentage nitrogen mineralization in casts (ΔN min as a percentage of total N). Native species are in bold.

Soil	Layer (cm)	Earthworm species	Ecto- or endo-nephridia	N total (%)	Mineral N (μg g^{-1})	(N min/N tot)%
Andisol[a]	0–5	Soil		15.5	516.8	
Martinique		***Species x***		14.8		5.2
		Pontoscolex corethrurus	Ecto	15.7	1095.1	4.2
		Polypheretima elongata	Endo	14.8	776.7	2.2
	5–10	Soil		12.7	423.5	
		Species x		12		9.9–15.7
		Pontoscolex corethrurus	Ecto	12.7	923.2	3.8
		Polypheretima elongata	Endo	13.5	606.6	2.3–3.3
	15–20	Soil		12.4	197.3	
		Species x		6.1		13.7
		Pontoscolex corethrurus	Ecto	6.1	536.7	5.5
		Polypheretima elongata	Endo			3.6
Andisol[b]	0–10	Soil		4.8	55.4	
Tuxtlas, Mexico		*Pontoscolex corethrurus*	Ecto	4.9	625.1	1.6
Luvic[c]	0–10	Soil		2.6	55.4	
Phaeozem, Cuba		*Onychochaeta elegans*	Ecto	2.4	212.5	6.4
Inceptisol[c]	0–10	Soil		0.9	17	13.9

La Vibora		*Pontoscolex corethrurus*	Ecto	1.1	173.5	13.3
Mexico		*Polypheretima elongata*	Endo	1.2	83.7	20.5
		***Glosso* sp.**	Ecto	1	220.4	17.2
Psamment[b]	0–10	Soil		1.1	12.3	
Mancha		*Pontoscolex corethrurus*	Ecto	1	183.6	13.3
Mexico		*Polypheretima elongata*	Endo	1	144.1	9.1
Ultisol[d]	0–10	Soil		1.37	30??	
Yurimaguas, Peru		*Pontoscolex corethrurus*	Ecto	1.47	150.5	9.1
Alfisol[e]	0–10	Soil				
Lamto, C.I		***Millsonia anomala***	Ecto			5.1
Vertisol[b]	0–10	Soil		3	52.1	
Laguna verde		***Protozapotecia australis***	Ecto	4	560.9	11.7
Mexico		*Pontoscolex corethrurus*	Ecto	4.2	199.5	3.7
		Polypheretima elongata	Endo	4.5	421.7	7.7
Vertisol[a]	0–10	Soil		1.84	225	
St Anne		*Pontoscolex corethrurus*	Ecto	1.8	758.7	29.7
Martinique		*Polypheretima elongata*	Endo	1.8	507.9	26.5

[a] Lavelle and Chotte (unpublished data); [b] Barois and Brown (unpublished data); [c] Martinez and Barois (unpublished data); [d] Lavelle *et al.* (1992); [e] Gilot-Villenave (1994).

Other nutrients

Earthworms affect other macronutrients such as Ca, K, Mg and Na, and also micronutrients. Many studies have shown that earthworm casts have increased concentrations of these elements or that they have been transformed to accessible forms for plant uptake; some of these studies have been carried out in the tropics (De Vleeschauwer and Lal, 1981; Mulongoy and Bedoret, 1989). The Ca ingested by earthworms is processed particularly by them because they possess calciferous glands or oesophageal regions which are involved in the production of $CaCO_3$. The increase of available Ca in fresh casts increases the pH which affects the concentrations of other soluble nutrients available for plant uptake (Blair *et al.*, 1994). Kale and Krishnamoorthy (1980) looked for Ca in the casts of *P. corethrurus* from Bangalore, India. They observed that the ionic (Ca^{2+}) and exchangeable Ca concentrations were 12 and seven times greater than in the control soil, respectively; conversely, the

Table 3.6. Exchangeable Ca, Mg, K and Na in soil and *Pontoscolex corethrurus* casts from four different soils of Veracruz, Mexico (n = 2; s = standard deviation).

	Nutrient (mEq 100 g^{-1})							
	Ca		Mg		K		Na	
	x	s	x	s	x	s	x	s
Plan de las Hayas Laguna Verde–Vertisol								
Soil	18.76	0.05	13.19	0.00	1.51	0.01	0.3	0.00
Pontoscolex corethrurus	20.89	0.27	15.20	0.00	0.63	0.00	0.54	0.01
Increase %	11		15		–58		80	
Tuxtlas–Andosol								
Soil	12.13	0.66	12.25	0.00	0.8	0.01	0.37	0.00
Pontoscolex corethrurus	14.25	0.00	12.37	0.00	0.85	0.03	0.55	0.00
Increase %	17		1		6		49	
La Mancha–Psamment								
Soil	21.84	0.13	8.5	0.00	0.38	0.01	0.2	0.00
Pontoscolex corethrurus	22.95	1.43	8.5	0.00	0.46	0.00	0.29	0.00
Increase %	5		0		18		45	
La Vibora–Entisol								
Soil	4.51	0.03	10.08	0.00	0.16	0.00	0.24	0.00
Pontoscolex corethrurus	4.49	0.15	10.05	0	0.2	0	0.29	0
Increase %	–1		–3		30		21	
Glossoscolecidae sp.	3.75	0.15	10.33	0.00	0.23	0.00	0.38	0.01
Increase %	–17		3		46		58	

All the data are the average of two replicates and rounded up to two decimals.

insoluble Ca was reduced by 82%. In *H. africanus* the increase in total content of Ca, Mg and K was 2.1, 1.3 and 3.3, respectively (Cook *et al.*, 1980). In Mexico, the exchangeable Ca, Mg, K and Na were measured in fresh casts of *P. corethrurus* from four different soils (Table 3.6). In most cases, the exchangeable cations increased in casts. The importance of these increments seemed to be linked to soil texture; if texture was fine, for example, in the Vertisol or the Andisol, the impact of the worm on the release of the exchangeable cations was more important than in soils with a coarse texture.

In the Entisol, the cast of the native Glossoscolecidae sp. had a higher content of exchangeable cations (Mg, K and Na) than the cast of *P. corethrurus*. This suggests, as observed for the mineralization of nitrogen, that native earthworms are better adapted to their original site and nutrient cycling than exotic species. These trends were not observed for exchangeable K; on the contrary, for this nutrient, there was either no effect of the worm or it even decreased its content in the casts. Similar observations were made by Abdul and Abdul (1996) for *Lumbricus terrestris* and by Basker *et al.* (1994) for *L. rubellus* and *Allolobophora caliginosa.*

Phosphorus

Earthworms also have significant effects on mineralization of P (see, for example, Sharpley and Syers, 1976; James, 1991; Lopez-Hernandez *et al.*, 1993; Chapuis and Brossard, 1995; Brossard *et al.*, 1996).

In our experiments, P extracted respectively with water (Pw), resin (Pres) and sulphuric acid 2 N (P-H_2SO_4) were significantly increased after transit through the earthworm gut. The largest difference was for water-extractable P, which was doubled after ingestion by the worms. In the three types of extraction, the P was at least 30% higher in the casts than in the soil. The earthworm effect on P was most notorious in the Alfisol of Lamto (Table 3.7; Brossard *et al.*, 1996).

A detailed analysis was done using a ^{32}P isotope in the Ultisol of Yurimaguas and the casts of *P. corethrurus* (Chapuis and Brossard, 1995). This technique demonstrated that the phosphate concentration of the soil solution and the pool of the immediately exchangeable ions associated with the soil increased in the casts; *P. corethrurus* selectively ingested fine soil particles and produced fresh casts which were more dispersable than control soil. These modifications in texture and structure led to a redistribution of P forms among size particles and chemical fractions (Chapuis *et al.*, 1996). The soil ingestion by earthworms promotes the transformations of P from the soil: the gut transit stimulates the mineralization of organic phosphorus into exchangeable forms.

Table 3.7. Phosphorus contents in different soils and earthworm casts assessed by water extraction (Pw), resin desorption (Pres) and sulphuric acid extraction ($P\text{-}H_2SO_4$ 2 N), with standard deviations in parentheses.

Soil	Layer	Earthworm species	Pw $(mg\ kg^{-1})$	Pres $(mg\ kg^{-1})$	$P\text{-}H_2SO_4$
Alfisol[a] (Lamto, Ivory Coast)	0–10	Control	2.2 (0.2)	4.9 (0.2)	20.3 (0.8)
		Hyperiodrilus africanus	5.3 (0.8)	10.4 (0.5)	37.4
		Chuniodrlus zielae	7.0 (0.6)	8.8 (0.4)	41.8 (2.7)
Ultisol[b] (Yurimaguas, Peru)	0–10	Control	0.4 (0.1)	4.9 (0.5)	22.8 (0.9)
		Pontoscolex corethrurus	1.9 (0.4)	8.5 (0.6)	39.8 (6.1)
Vertisol[c] (St Anne, Martinique)	0–10	Control	13. (0.5)	12.8 (1.7)	269.1 (10.1)
		Pontoscolex corethrurus		36.6 (4.5)	343.8 (11.9)
		Polypheretima elongata	19.5 (0.5)		

[a]Lopez-Hernandez *et al.* (1993) and Lavelle, unpublished data; [b]Chapuis *et al.* (1996); [c]Brossard *et al.* (1996)

Conclusion

Detailed surveys of demographic parameters and short-term effects of 26 native and exotic species have allowed a description of the mechanisms of various species and comparison of their efficiency.

PCA permitted four groups of species to be separated on the basis of their demographic parameters. Species with potential for manipulation in agroecosystems are found mainly in group 3, which comprises species of a relatively small size (170–1250 g), with generation times of 3–7 months and fecundity rates of 10–68 cocoons adult^{-1} year^{-1}. Group 2 has larger species with characteristics intermediate between those of groups 1 and 3.

In a given group, exotics tend to have shorter generation times and higher fecundity rates than natives. All of them are parthenogenetic, at least facultative. Their ability to increase the density of their population rapidly, and parthenogenesis, which allows a single individual to build a population, contribute to the explanation of their success in disturbed environments. Efficient mutualistic interactions with the soil microflora, indicated by high amounts of intestinal mucus in the gut, facilitates SOM digestion and may contribute to the success of these species in colonizing environments with highly variable OM quality and content.

However, one of the most difficult parameter to determine for a successful earthworm population growth is its food, particularly for mesohumic and oligohumic species. Some of the selected species with environmental tolerance, found in natural and managed ecosystems, were hard to cultivate in laboratory conditions, e.g. *M. anomala* (Ivory Coast), *Z. guapotus* (Mexico) and *R. pashanasi* (Peru). Some work needs to be done in this direction.

Up to now, the species that seem more amenable to manipulation are those that are cultivated easily in laboratory conditions; most of them are exotic and their feeding habits are polyhumic or polymesohumic, e.g. *P. corethrurus*, *P. elongata* and *B. pearsei*, although other species from different ecological categories, such as *H. africanus* (epiendogeic) in Africa and *D. bolaui* (epigeic) worldwide, have shown a great ecological plasticity (Fragoso *et al.*, Chapter 2) and ability to be cultivated. More data are needed on demographic parameters and short-term effects of native species, especially those found in managed ecosystems.

The species with a high potential to be manipulated have an aggregate spatial distribution. Thus, on a short time scale, earthworm populations can display a localized or heterogeneous effect. The spatial behaviour of a given species is related to its demographic and morphological characteristics and hence may be included in the definition of the ecological categories.

Short-term effects of earthworms on soil include:

1. High rates of soil ingestion; annually several hundred megagrams of dry soil are ingested by the earthworm community, and egested as surface subterranean casts.
2. Selective ingestion of soil particles; they generally select small mineral and large organic particles; however, in clay soil rich in organic matter, they tend to select sand rather than small particles.
3. Dispersal of microorganisms and seeds; they particularly promote the dispersal and infection of VAM and contribute to the formation and conservation of the seed bank.
4. Mineralization of N and P from soil organic matter; 1.6–29.6% of organic N is mineralized as a result of digestion and futher mineralization in fresh casts. When comparisons were possible, native species promoted higher mineralization than exotics. This is an important issue for further research on native species with the possibility to be manipulated. Earthworms also promote the availability of others nutrients such as Na and Ca.

The earthworm characteristics, biological and ecological, are summarized in Fig. 3.11, as well as their effects on soil properties and processes. It can be remarked that they affect the soil dramatically, altering it in many ways. At the population and community level, the effects can be magnified or complementary. Thus, by manipulating the earthworm community, soil fertility can be ameliorated for example. Further examples and experimental results will be given in Chapters 4, 5 and 6.

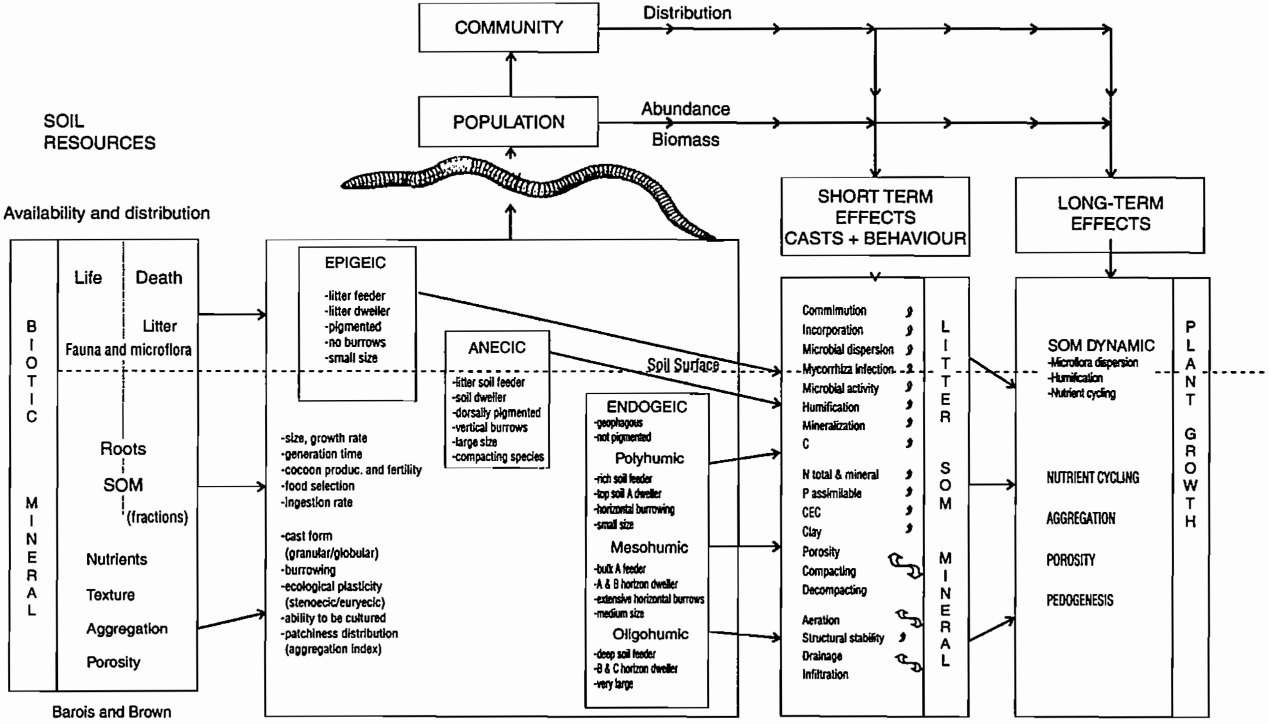

Fig. 3.11. Ecological and biological earthworm characteristics and their effects on soil properties. The earthworms characteristics are influenced by soil resources (food and habitat). They have in their turn effects on soil properties and thus can be positive or positive and negative. They act individually, or at population and community levels. Their impact is from the soil surface to the deeper soil horizon, and is linked to time (short- and long-term effects).

Acknowledgements

We would like to thank Soraida Irisson for technical help, and Ron de Goede and José Antonio Garcia Perez for their comments on the principal components analysis.

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Effects of Earthworms on Plant Production in the Tropics

4

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Summary

As part of the European Union-funded Macrofauna Project, 16 experiments were conducted over a 7-year period on the effects of earthworm inoculation on plant production, both at the greenhouse and field level. These experiments were undertaken in six countries, involved 14 plant species, six great groups of soils, and at least 13 species of earthworms. Additional data were taken from the literature, totalling > 240 data points on the percentage change (±) in above-ground production in the presence of more than 34 earthworm species. The overall average increase in shoot and grain biomass due to earthworms was + 56.3% ± 9.3% (SE) and 35.8 ± 8.9%, significant at $P < 0.07$ and $P < 0.08$, respectively. Highest increases were observed in soils with sandy textures, poor in organic matter, and with a moderately acid pH.

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(eds P. Lavelle, L. Brussaard and P. Hendrix)

Earthworm biomass of around 30 g m^{-2} or more was shown to be necessary to promote agriculturally important (> 40%) grain yield increases. Earthworm species which appeared most promising in enhancing plant growth at both the field and pot experiment levels were *Pontoscolex corethrurus* and *Drawida willsi*, both introduced with substantial results in India. Several other species showed significant advantages in particular situations, and are likely to be useful under wider conditions of crop and soil management. Plants most affected were tropical trees (in Peru), tea in India, and *Panicum maximum* grass, planted both in Australia and the Ivory Coast. Benefits of earthworm introduction are, therefore, particularly important in perennial cropping systems. Large and significant increases in grain biomass were observed in several situations, especially for sorghum, rice and maize. Leguminous crops appeared to be less enhanced by earthworm activities.

Numerous mechanisms are involved in plant growth stimulation (observed in 72% of all cases), ranging from large-scale effects on soil physical properties (aggregation and water infiltration), to the microsite level where earthworms enhance microbial activity, nutrient availability and rhizosphere processes. When earthworms are to be introduced, a suite of adapted species, at sustainable numbers and biomass, must be added to ensure a stable population which will induce favourable soil properties and enhanced plant production. Once earthworms are established, cropping systems involving crop rotations with long-cycle crops or perennials with sufficient organic matter additions will help secure long-lasting benefits from earthworm activities.

Introduction

The importance of earthworms for plant growth has been recognized for over 100 years, since the publication of Charles Darwin's book *The Formation of Vegetable Mould Through the Action of Worms* in 1881. Over the last century, many researchers, primarily in the temperate zone, have described the effects of earthworms on plant production, at the field and small-scale (pot) levels. Their experiments (summarized in Blakemore and Temple-Smith, 1995) dealt almost exclusively with four to six widespread lumbricid earthworm species in pasture or cereal crop situations. The results show that these earthworms exert primarily beneficial effects on plant growth, although in a few cases, negative or null effects could be induced under particular situations. In addition, shoot biomass tended to benefit more than roots from earthworm activities.

Nevertheless, various shortfalls have become obvious from these studies. Pot trials are run generally for relatively short periods of time (only one crop cycle), often receive unrealistically high earthworm densities and biomass or are performed using earthworm casts or composts rather than live earthworms, and the earthworm species used are often not identified adequately. In field experiments, there is little control over many variables, it is difficult to completely exclude earthworms from control plots, and earthworm structures produced before the trials are long-lasting, possibly masking current earthworm exclusion treatment effects. Also, there currently are over 3000 earthworm species classified, and probably an equal or larger number still to be described, many of which appear to have some potential for management in tropical agroecosystems (Chapter 1). It is thus essential that more species be tested for potential effects on plant production, particularly in the tropics where a limited number of studies has been conducted using common tropical earthworm species and plants. Given that much of the world's population lives in, and their food production originates from this zone, it is imperative that more attention be paid to understanding the role of tropical earthworms (both native and exotic, widespread and locally common species; Chapter 1) in enhancing production of tropical food, fodder and tree crops.

Objectives

Following the above demands for information, and the need for further research in this area, during the 6 years of research of the 'Macrofauna' programme, various experiments both at the glasshouse and field level were performed on the influence of earthworms on soil fertility and plant growth. This chapter synthesizes the data obtained and, together with other experiments performed both before and after the programme began, attempts to address the following questions:

1. Are earthworms in the tropics important for plant growth and, if so, to what degree?
2. What plant species (trees, crops, grasses, etc.) are affected the most, and by which species of earthworms?
3. By what means (the mechanisms) are plants affected by earthworm activity, positively and negatively?
4. How many earthworms, or what biomass is necessary to have a measurable (and agriculturally important) positive effect?

Materials and Methods

Experimental designs

To address these questions, soil biological, physical and chemical parameters, earthworm survival and production of different plant parts (above- and belowground) were evaluated to reveal mechanisms of plant growth enhancement (if observed) in 16 experiments completed during the Macrofauna programme. A review of the literature for the tropics revealed a further 12 trials which had suitable data on earthworms and plant biomass for the statistical analyses

(Senapati *et al.*, 1985, unpublished data; Spain *et al.*, 1992; Blakemore, 1994; Kobiyama, 1994; dos Santos, 1995; Patrón, 1998). Thus, in 28 experiments chosen, at least 34 earthworm and 19 plant species were tested in approximately 23 different soils belonging to eight great groups. For each of these experiments, selection criteria were applied to determine which earthworm, soil type and crop species would be used. Earthworm species used were common at or near the site, and known to be generally adaptable to cropping systems and to affect soil properties. In general, the soils used were C-poor, often having some kind of deficiency or limitation for crop growth, although in a few cases, C-rich soils (e.g. pasture or forest soils) were used. The characteristics of the soils used in the experiments are given in Table 4.1. Finally, the crops tested were ones that were widely sown by farmers in nearby regions. Since much of the food consumed in the tropics is grown at household or small field levels for self-subsistence or local markets, and few external inputs are added to the cultivated plants, low-input practices were usually mimicked in the experiments detailed below. A brief summary of the main materials and methods used is shown in Table 4.2.

Generally speaking, the trials were performed at three levels, spatially and temporally.

1. At the smallest scale, short-term experiments lasting from 15 days to 8 months, using various containers (nursery bags, buckets, PVC pipes) and involving either one or two cropping cycles were performed in the greenhouse and open air. More than 12 plant and at least 27 earthworm species were tested in small to medium volumes of soil (oven dry weight from 0.9 up to 17.5 kg) of approximately 12 different types. The purpose of these experiments was to reduce soil and climatic variability, illustrate the mechanisms of earthworm effects on soil and plants in greater detail, and find the most promising earthworm and plant species associations to use in field situations. The plants tested had different rooting strategies (fibrous or taproot) and life cycles (short or long season, perennial), and the earthworms were of various ecological strategies (mostly endogeic, some epigeic and anecic).

2. At the intermediate scale, 13 species of earthworms were inoculated into field plots with and without enclosures which isolated a set volume of soil. Plot size varied from circular plots of 60 cm diameter (0.28 m^2) at Yurimaguas (Peru) to 50 m^2 at St Anne (Martinique). Earthworm biomass added varied greatly but, for most cases, equivalent values found nearby were taken as a basis. More than eight plant species were tested for periods lasting from 4 months to 7 years. Several trials were performed with similar plant and earthworm species used in the smaller scale experiments to confirm that previously observed effects would also be present at field scales (e.g. in Ivory Coast, Australia and India).

3. At the broadest scale, earthworms were reared in special culture beds and introduced *en masse* into the field, to assess their colonization potential and effects on plant production in a situation more comparable with farmers' fields.

Table 4.1. Types and characteristics of soils used in field and greenhouse investigations on the role of earthworms in soil fertility and plant production.

Soil type	Location	Vegetation	Rainfall (mm)	% Sand	% Silt	% Clay	% C	% N	C/N	pH	CEC (mEq 100 g^{-1})	Reference
Ferralsol (Alfisol)	Lamto, Ivory Coast	Savanna	1228	75.4	14.0	7.5	1.09	0.08	14.3	n.d	3.2	Spain *et al.* (1992)
	Lamto, Ivory Coast	Secondary forest	1228	87.6	8.5	4.7	1.26	0.13	9.9	7.5	5.1	Gilot (1994)
	Lamto, Ivory Coast	Savanna	1228	78.1	17.0	6.0	0.91	0.05	17.3	6.7	4.4	Gilot (1997)
	Lamto, Ivory Coast	Secondary forest	1228	85.0	10.5	4.5	1.18	0.12	9.8	7.15	5.3	Gilot *et al.* (1996)
	Lamto, Ivory Coast	Savanna	1228	72.6	12.1	11.7	0.91	0.11	14.1	7.5	n.d	Derouard *et al.* (1997)
Psamment	La Mancha, Mexico	Weed fallow	1345	75.4	8.6	16.0	1.65	0.11	15.7	7.9	30.9	Patrón *et al.* (unpublished data)
Andosol	Los Tuxtlas, Mexico	Tropical rainforest	4700	18.5	37.4	41.9	5.27	0.46	11.4	5.9	13.5	Brown *et al.* (unpublished data)
Inceptisol	La Vibora, Mexico	Savanna–pasture	1400	81.5	7.4	10.6	1.07	0.10	10.7	5.1	12.1	Brown *et al.* (unpublished data)
Ultisol	Mbalmayo, Cameroon	Secondary forest	1600	61.8	16.0	22.2	4	n.d.	n.d.	6.34	n.d.	Brussaard *et al.* (unpublished data)

Table 4.1. *Continued*

Soil type	Location	Vegetation	Rainfall (mm)	% Sand	% Silt	% Clay	% C	% N	C/N	pH	CEC (mEq. 100 g^{-1})	Reference
Typic paleudult	Yurimaguas, Peru	Secondary forest	2100	55	22	23	1.68	0.13	12.9	4.0	5.5	Pashanasi *et al.* (1994)
	Yurimaguas, Peru	Secondary forest	2100	67.7	23	9.1	2.07	0.13	15.9	4.17	5.14	Chapuis (1994)
	Yurimaguas, Peru	Secondary forest	2100	59.1^a 54.3^b	22.1 23.6	19 22	1.55	0.11	14.1	4.3	n.d.	Pashanasi *et al.* (unpublished data)
Eutric vertisol	St Anne, Martinique	New pasture	1580	25	15	60	1.4	0.14	10	6.25	37	Hartmann *et al.* (1998)
Vertisol	Sambalpur, India	Rice paddy field	1500–2000	92.6	1.52	5.88	1.44	0.23	6.48	7.21	3–5	Senapati *et al.* (unpublished data)
	Sambalpur, India	Rice paddy	1500–2000	92.8	1.4	5.8	1.43	0.22	6.5	7.1	3–5	Senapati *et al.* (1985)
Oxisol	Tamil Nadu, India	Deciduous forest	2000–3000	60–70	n.d.	30–40	1.77	0.19	9.3	6.4	4–9	Giri (1995)
	Tamil Nadu, India	80-year-old tea culture	2000–3000	65.6	19.3	9.93	1.34	0.24	5.2(?)	6.58	4–9	Giri (1995)
Oxisol	Curitiba, Brazil	Fallow	1400	46	14	40	6.1	n.d.	n.d.	n.d.	23.3	Kobiyama (1994)

Oxisol	Guarapuava, Brazil	Wheat	1880	17.8	44.2	38	4.2	n.d.	n.d.	n.d.	19.4	dos Santos (1995)
Vertisol	Narayen, Australia	*P. maximum* pasture	710	13	23	43	4.8	0.35	13.7	7.0	38	Blakemore (1994)
	Biloela, Australia	No-till sorghum	600	20–45	n.d.	>30	2.4	0.145	16.6	7.9	n.d.	Blakemore (1994)
Oxisol	Kingaroy, Australia	*P. maximum* laneway	n.d.	n.d.	n.d.	55–60	n.d.	n.d.	n.d.	5.5	n.d.	Blakemore (1994)
Ultisol	Samford, Australia	20-year-old grass pasture	1105	82	4	10	1.3	0.08	16.3	5.7	8.6	Blakemore (1994)
Mollisol	Samford, Australia	Mixed-sward pasture	1105	34	17	42	6	0.33	18.2	6	30	Blakemore (1994)

[a] Earthworm-inoculated treatment; [b] non-inoculated treatment.

Table 4.2. Simplified summary of materials and methods used for experiments performed to assess the role of earthworms in plant production.

Scale	Site	Duration	Plants tested	Earthworm species used	Mass added (g m^{-2})	Reference
Nursery bags	Yurimaguas, Peru	15 days–8 months	Fruit trees (three species)	*P. corethrurus*	3.5–22	Pashanasi *et al.* (1992), Ydrogo (1994)
	Tamil Nadu, India	120, 150 days	Tea	*P. corethrurus*	127	Giri (1995)
Buckets	Lamto, Ivory Coast	79, 84 days	Maize, *Panicum maximum*	*P. corethrurus, H. africanus, M. anomala, C. zielae, S. porifera*	12.5–128	Spain *et al.* (1992)
		69–74 days	Peanuts, rice maize		56.5	Derouard *et al.* (1997)
	Xalapa, Mexico	30 days–6 months	Beans, maize	*P. elongata, P. corethrurus*	32–63	Brown *et al.* (unpublished data)
	La Marquesa, Mexico	90 days	*Brachiaria decumbens*	*P. corethrurus*	114	Patrón (1998)
	Mbalmayo, Cameroon	65 days	Maize	At least two species	164	Brussaard *et al.* (unp. data)
	Sambalpur, India	~90 days	Rice	*D. willsi*	42.4	Senapati *et al.* (1985)
PVC tubes	Brisbane, Australia	26 days–30 months	Oats, sorghum, three grass species	At least 27 different species	13.5–326	Blakemore (1994)

Single crop cycle field studies	Lamto	35–90 days	Maize	*M. anomala*	52	Gilot (1994, 1997)
	Sambalpur	90 days	Rice	*D. willsi*	13	Senapati *et al.* (unpublished data)
	Narayen,	14.5 months	*P. maximum*	Nine species	8–166	Blakemore (1994)
	Samford	13.2 months	Various grasses	Ten species	7–166	
	Curitiba, Brazil	9 months	*Mimosa scabrella*	*Amynthas* spp.	30–90	Kobiyama (1994)
Multi-crop field enclosures	Lamto	3 years	Yam, maize	*M. anomala*	16–31.4	Gilot (1994)
	Yurimaguas	3–7 years	Rice, cowpea, maize	*P. corethrurus*	36	Pashanasi *et al.* (1994, 1996), Charpentier (1996)
	La Mancha, Mexico	3 years	Maize	*P. corethrurus* (*P. elongata*)	35.5	Patrón *et al.* (unpublished data)
	Guarapuava, Brazil	1 year	Beans, wheat	*Amynthas* spp.	30–90	dos Santos (1995)
Long-term field inoculation	Yurimaguas, Peru	3 years	Maize, cassava, cowpea, trees	*P. corethrurus*	1–36	Pashanasi *et al.* (unpublished data)
	Tamil Nadu, India	>3 years	Tea	*P. corethrurus* + four species	648	Giri (1995)
	St Anne, Martinique	>4 years	Pangola (*Digitaria decumbens*)	*P. elongata*	~90	Blanchart (1997)

In addition, costs and benefits of such large-scale undertakings were studied to reveal the economic viability of such ventures (Chapter 7). Results from these studies would be immediately applicable to situations common around the research sites. Two trials were performed at this level, one in Lower Sheikalmudi, in the state of Tamil Nadu, India, and the other, at Yurimaguas, Peru (see Chapter 7 for details). At the first site, 1200 pits of 0.54 m^2 each were dug in one hectare including 5500 tea trees approximately 80 years old. A large quantity of residues and four species of earthworms (primarily *Pontoscolex corethrurus*) were applied at the rate of about 150 kg ha^{-1} (350 g pit^{-1}), in half of the pits and tea production studied intensively over a 10-month harvest cycle (Giri, 1995). At Yurimaguas, a forest area of about 0.5 ha was cleared, and two areas, one receiving earthworms and one not, were separated by a pesticide-poisoned soil strip. Two types of agricultural practices, traditional (shifting cultivation) and 'improved' (use of fertilizers), were applied to the area, and *P. corethrurus* was inoculated at the rate of 1–10 g m^{-2} on several planting dates (e.g. together with maize seed), on top of the resident earthworm fauna. During the 3-year trial, maize, rice, cowpea, cassava and forest trees were planted, depending on the system. Unfortunately, the soil textural difference between inoculated and uninoculated plots (Table 4.1) led to a low survival of inoculated earthworms in addition to greater crop harvests in the control treatments, so the experiment had to be abandoned.

One of the most pernicious problems in performing both pot and field experiments was preventing contamination of control plots with resident or introduced earthworms. For instance, in La Mancha, plots inoculated with *P. corethrurus* were contaminated increasingly with *Polypheretima elongata*. Several methods were imposed to prevent contamination and to kill or remove resident or potential invading earthworms, with variable effectiveness. The most efficient methods utilized were to sterilize the soil by heating (for pots), to choose sites with low native earthworm populations (e.g. Narayen, Australia, for pots and field; Blakemore, 1994) or to extirpate them chemically with carbamate pesticides (e.g. Lamto, St Anne and Yurimaguas). The least effective method was soil tillage and/or hand removal (e.g. La Mancha).

Data analyses

For the statistical analyses, data on earthworm biomass initially applied and at (each) harvest, the plant biomass obtained in each treatment (in units of Mg ha^{-1}), the plant and earthworm species tested, plot size, amount of residues applied and the characteristics of the soils (percentage sand, silt and clay, % C and pH) used in the 28 experiments were entered on to a spreadsheet. Analysis of variance (ANOVA) and principal component analyses (PCA) were conducted using the previous factors and the percentage increase in plant biomass in the earthworm-inoculated versus non-inoculated treatments (controls) for each of the plant parts studied (e.g. grain, stubble, root).

Results and Discussion

Identification of major factors

A total of 246 data points, means of specific treatments resulting from 28 different experiments were obtained for total above-ground (shoot) plant parts. In contrast, fewer data were available on grain production as well as root or total plant biomass (Table 4.3). The overall percentage increase due to earthworms was higher for total shoot biomass (56.7%) than for grain alone (35.8%). However, due to the high variability of the results (see Appendix 4.1 for details), both effects were significant only at $P < 0.08$. Similarly, the high increases observed in root and total plant biomass production were not significantly different from the no-worm controls (Table 4.3).

The percentages of instances in which shoot and grain production increased in response to earthworm inoculation were 75.2 and 71.6%, respectively (Table 4.3). In the frequency histogram of the results of shoot biomass (Fig. 4.1), about half of the results fell within –20% to +20%, where earthworm effects are not so important (and rarely significant). The other half of the results fell within a range where earthworm effects became increasingly important, i.e. more than +20% or less than –20%. Of these, most were positive effects, contributing 43% of the total, only 5% being negative. These results show that the effect of earthworms on above-ground production is generally positive, and in many cases may be highly so, but also that it may be near to neutral (no effect, or unimportant, both positive and negative) in a

Table 4.3. Summary of overall percentage increases in biomass of different plant parts, with standard error of the mean (SE) and *P*-value of the increase due to earthworm presence. In addition, the frequency of biomass increase or decrease is shown using all available data (number of experimental results used shown under 'n').

Plant part	*n*	Overall % increase[a]	SE	*P*-value	Increases (%)	Decreases (%)
Shoot	246	56.7[b]	9.31	0.07	75.2	24.8
Grain	88	35.8[b]	8.88	0.08	71.6	28.4
Root	115	66.1[a]	21.8	0.83	59.1	40.9
Total	116	62.8[b]	18.8	0.42	74.6	25.4

[a] Values with the same letters are not significantly different from each other at $P < 0.05$.

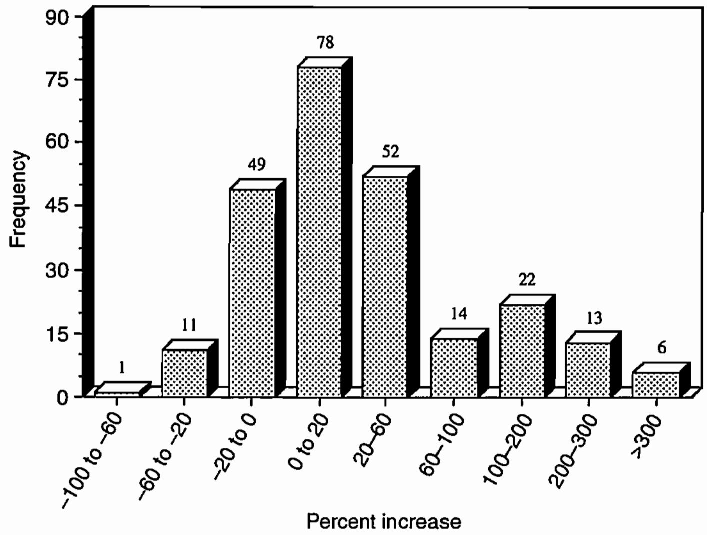

Fig. 4.1. Histogram of the frequency of increases in above-ground (shoot) plant biomass due to earthworms (the numbers above the bars indicate the number of cases). Data from the Macrofauna and other available experiments performed in the tropics (246 data points).

large number of cases. An important finding was that above-ground plant biomass is rarely greatly reduced by earthworms, such phenomena occurring only under specific circumstances (explained later in the text). Root production, on the other hand, was skewed partially to the negative, neutral and unimportant increase values. Over 40% of the results were negative (reduction in root biomass), and 60% had increases of 20% or less.

Factors that control these responses, and the variability of earthworm effects were explored using PCA analysis of the shoot results including 221 data points. The analysis showed that the percentage increase due to earthworms was correlated positively with residue applications and sand content, and inversely related to clay and C contents of the soil (Table 4.4). However, correlation coefficients of residues and sand with the percentage increase were low (0.42 and 0.11, respectively). Earthworm biomass applied had no particular relationship to shoot biomass increase. The first principal component (FI) of the analysis corresponded mostly to soil factors (texture and C content) and accounted for 43.9% of the explained variance, while the second component (FII) was related to OM (organic matter) applications and the percentage increase accounting for 18% of the variance. A similar analysis was performed with 89 data points on grain production, and yielded different results: few variables were closely correlated to the percentage increase, the most related being earthworm biomass applied (correlation coefficient = 0.17) and biomass recovered (cc = 0.20) at the end of the experiment. These

Table 4.4. Correlation coefficients between the different factors and the shoot production increase and earthworm biomass applied, resulting from the principal component analysis (PCA) using a total of 221 data points on shoot biomass percentage increase, earthworm biomass and quantity of residues applied, and the soil's texture, %C and pH.

Factors	Shoot % increase	Earthworm mass applied
Residues	0.42	0.10
% increase	—	0.20
Mass applied	0.02	—
Sand	0.11	–0.18
Silt	0.04	0.05
Clay	–0.24	0.24
%C	–0.21	0.14
pH	0.01	0.14

analyses appear to point to the important role of earthworm biomass, residue applications and the soil's percentage C and texture in governing the role of earthworms in plant production. These were explored further using ANOVAs (below).

To understand further the differences in the results obtained, the soils of all the experiments were separated into three distinct classes according to texture, OM content and pH, and the percentage increase due to earthworm activities was calculated for the different plant parts in each of the soil classes. Sandy soils had >65% sand and < 10% clay, clayey soils had > 30% clay, and intermediate soils grouped all the other textures represented. C-poor soils had < 1.5% C, C-intermediate soils 1.5 < % C < 3 and C-rich soils > 3%C. Strongly acid soils had pH < 5.6, moderately acid soils 5.6 < pH < 7.0 and alkaline soils pH > 7.0. The results, presented in Fig. 4.2 and Table 4.5 show significant differences in earthworm effects depending on the plant part as well as the soil status. The increase of the different plant parts was higher in C-poor and intermediate than C-rich soils, and in sandy than in loamy or clayey soils. Regarding pH, the percentage increase was higher in moderately acid and strongly acid than alkaline soils. Earthworm effects, therefore, seem to be particularly enhanced in sandy soils, with less than 10% clay, in strongly to moderately acid soils with pH < 5.6 up to 7, and in poor-C status soils, with < 1.5%C.

Several separate analyses confirm the above observations. For example, in Yurimaguas, when no residues were applied, the average increase in grain production due to *P. corethrurus* was + 46%, but when crop residues

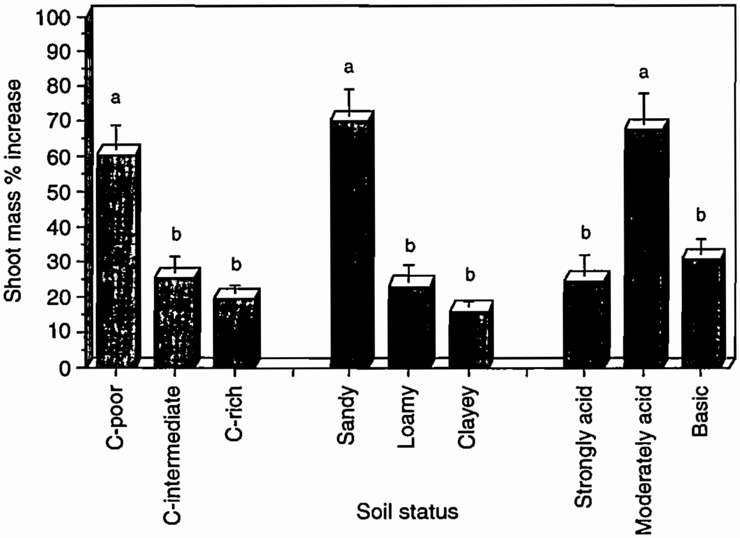

Fig. 4.2. Average percentage increase (+ SE bars) in above-ground (shoot) production due to earthworm activities in relation to soil texture, richness (%C), and pH, taken from a total of 221 data points. Poor soils had < 1.5%C, rich soils, > 3%C, and intermediate soils, 1.5 < %C < 3; sandy soils had > 65% sand and < 10% clay, clayey soils had > 30% clay, and intermediate soils, all other textures represented; strongly acid soils had pH < 5.6, basic soils, pH > 7.0, moderately acid soils, 5.6 < pH < 7.0. Bars with different letters indicate significant differences at $P < 0.05$.

(additional C inputs) were applied it was reduced to + 21%; when both residues and green manure were added, it was even lower, at + 15% (Pashanasi *et al.*, 1996). When all available data for pasture grass species were analysed separately, average shoot and root biomass increase due to earthworms was calculated to be 72% in C-poor sandy soils, while in C-rich (clay) soils it was 24%, although the production gain due to earthworms was similar (1–1.2 Mg ha^{-1}). Root biomass change in the same soils was + 50.5% (C-poor) and −11.2% (C-rich), respectively, indicating that in C-rich soils, earthworms tended to have a slight negative effect on roots. When all rice grain biomass data were combined, the increase was found to be higher in sandy (86.8%) than in loamy (30.7%) soils, even though (as for the pastures) average production increase in both soils was similar, approximately 0.2–0.3 Mg ha^{-1} higher in earthworm treatments. Although both the pastures and the rice had different earthworm species and biomasses applied, and the different responses may be due to factors other than the soils involved, these results highlight the importance of soil factors on the effect of earthworms on plant biomass. Several reasons may account for these phenomena. First, soil nutrient reserves in no residue treatments and in C-poor and sandy soils are lower than in the other treatments, where the earthworm effects may be diluted by nutrients in residue inputs. Secondly, earthworms such as *P. corethrurus* are able to exploit

Table 4.5. Percentage increase in biomass of different plant parts due to earthworms depending on the percentage carbon, texture and pH of the soil utilized. Values with different letters within a same column indicate significant differences at $P < 0.05$.

	Plant part		
	Shoot	Grain	Root
Soil status		Increase (%)	
C-poor	60.5^a	29.9^a	22.6^b
C-intermediate	25.5^b	47.2^a	48.9^a
C-rich	19.9^b	7.7^a	−14.1^c
Sandy	70.0^a	53.2^a	33.4^b
Loamy	23.3^b	24.4^a	24.1^b
Clay	16.2^b	29.0^a	11.7^{bc}
Strongly acid	24.9^b	38.3^a	35.9^b
Moderately acid	67.5^a	(22.4)^{a1}	28.6^b
Basic	30.9^b	33.8^a	15.3^{bc}

[1] $n = 1$.

highly stable organic reserves in poor soils with the help of microorganisms (Barois and Lavelle 1986; Lavelle and Gilot, 1994), thus liberating and cycling nutrients that would otherwise be tied up and unavailable to plants.

Species-specific responses

Plant species

The combined effect of all earthworm species together on the shoot biomass of each plant species in both field and pot trials is shown in Fig. 4.3. Despite several large increases in biomass, only a few plants showed significant earthworm treatment effects, due to the high variability between different experiments. The lack of significance at this level of analysis, therefore, does not imply that earthworm effects on biomass were not significant at the individual experiment level (in fact, this was very often the case, particularly in pot experiments). Rather, it shows that combining all the mean plant biomass yields (in Mg ha^{-1}) from each trial with the same species resulted in no significant differences between biomass of treatments with and without earthworms.

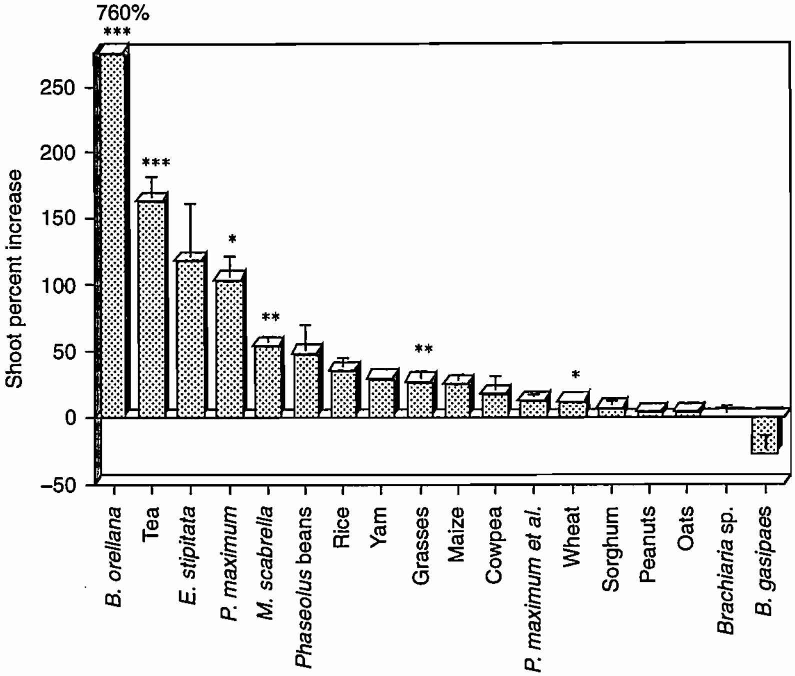

Fig. 4.3. Percentage increase (mean + SE bars) due to all earthworm species combined, of above-ground biomass of 17 plant species (from a total of 246 data points). Statistical significance of the *F*-test comparing the means of earthworm and non-inoculated treatments are shown as follows: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$. (Note: grass species tested were *Digitaria didactyla* and *Cynodon, Paspalum* and *Setaria* spp. The species harvested with *P. maximum* were *Chloris gayana* and *Cenchrus ciliaris*; *Brachiaria* species used was *B. decumbens*.)

The plants most positively affected by earthworm activity were the trees *Bixa orellana* (760.7%), *Eugenia stipitata* (117%), tea (162%) and *Mimosa scabrella* (53.7%), and the pasture grass *P. maximum* (103%), the production increase being equivalent to 1.7 Mg ha^{-1} (in a single cut) for the latter plant. Interestingly, these are all perennial plants. Little work other than the studies mentioned here has dealt with the effect of earthworms on perennials in the tropics, and more work is warranted. Shoot biomasses of annual crops were less affected, the highest increases being those found for common beans and rice (47.9 and 35%, respectively, though the effects were not statistically significant). In Australia and Brazil, significant increases (15.6 and 11.5%, respectively) were observed at the field level for four pasture grasses and wheat, showing production gains of approximately 0.8 and 0.4 Mg ha^{-1}, for each trial, respectively, due to earthworms.

Only the palm tree *Bactris gasipaes* responded negatively to earthworm activity in the nursery bags, due to its coarse root system being perhaps unable to take advantage of worm structures which increased soil compaction and reduced water infiltration. Similar growth reductions were encountered for crops such as oats, maize and rice in other individual experiments (Blakemore, 1994; Gilot, 1994; Pashanasi *et al.*, unpublished data), although the reasons for these decreases were not well explained. The occurrence of and mechanisms by which earthworm activity leads to decreased plant production are poorly understood and need further research.

Grain production was increased by earthworms in five of the seven annual crops tested (Fig. 4.4), although a significant increase was only observed for sorghum (59%, equivalent to a 1.44 Mg ha^{-1} production gain). Grain biomass increases for rice and maize were more than 42%, but the combined differences over all the studies (~0.2 Mg ha^{-1} more grains with earthworms in both crops) were not significant. Yields of leguminous plants were little affected (beans), or negatively affected by earthworm activities (peanuts and cowpea), while graminaeous grain crops were always affected positively. Reasons for this may be different (generally higher) nutrient demands and root architecture, and the lack of symbiotic N_2-fixing microorganisms in the grass crops, i.e. greater N independence in the legumes. Further mechanisms may involve symbiotic or other organisms (e.g. mycorrhizae, protozoa, nematodes, parasitic fungi) affected directly or indirectly by earthworm activities (see later discussion).

Effect of earthworm species

Increases in shoot biomass due to the presence of different earthworm species varied substantially (Table 4.6). Intraspecific variation in the results was also high, depending on the crop, soil type and experimental conditions; only in one case (*P. corethrurus* + *Notoscolex* sp., *Metaphire* sp., *Megascolex* sp. and

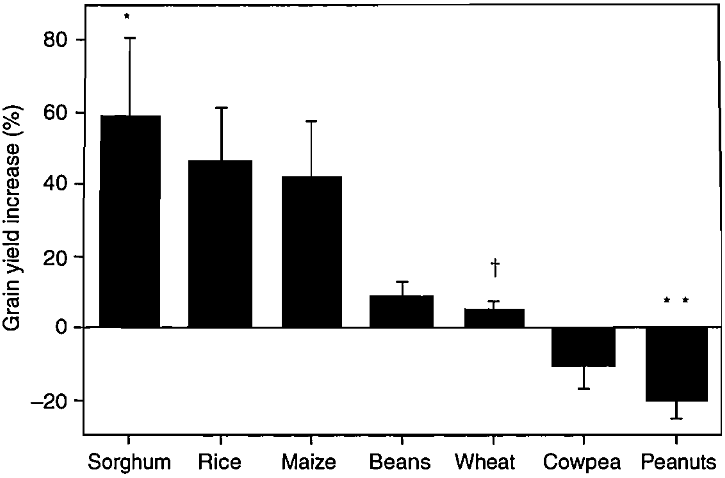

Fig. 4.4. Average percentage increase (+ SE bars) in grain biomass of seven annual crops due to earthworms (from a total of 89 data points). Statistical significance, when applicable, shown above the column ($^{\dagger}P < 0.1$); significance values as in Fig. 4.3.

Table 4.6. Average plant shoot biomass increase due to earthworm species or species combinations, mean earthworm survival rates, percentage of positive results (increases) obtained from the total number of observations (*n*), crops most positively affected and the potential of each species for management or introduction into tropical or subtropical cropping systems. Rows are arranged according to shoot percentage increase, in decreasing order.

Earthworm species (ecological category)	Location	Crops most affected[a]	n[b]	Shoot increase (%)	*P* value	Change in mass ($g\ m^{-2}$)	Mean survival (%)	Positive results (%)	Potential (see text)
Pontoscolex corethrurus + others[c]	India	Tea	20	217.4	0.0001	−585.3	9.7	100	High[d]
Pontoscolex corethrurus (mesohumic endogeic)	Peru, Mexico, India, Ivory Coast, Australia	Tea, trees, maize, rice	69	81.8	0.45	+22.6	323.4	65	High
Chuniodrilus zielae + *Stuhlmania porifera* (polyhumic endogeics)	Ivory Coast	*Panicum*, maize	6	69.1	0.37	−5.6	123.3	100	High
Drawida barwelli + *Amynthas minimus*	Australia	Grasses	2	63.6	0.298	−23.9	0.32	100	Low
Millsonia anomala (mesohumic endogeic)	Ivory Coast	Maize, yam, *Panicum*	29	58.2	0.38	−1.0	98.9	63	High
Undetermined endogeics (at least three spp.)	Cameroon	Maize	2	45.2	0.63	?	n.d	100	?
Heteroporodrilus bongeen	Australia	Oats	1	39.6	–	−253.3	0	100	Low
Polypheretima elongata (mesohumic endogeic)	Mexico, Australia	Beans, sorghum	9	35.4	0.84	+19.1	126.7	50	Medium

Aporrectodea trapezoides + *Eisenia rosea*	Australia	Grasses	2	29.7	0.59	−164.0	1.2	100	Low
Diplotrema sp. nov. 1	Australia	Grasses, oats	9	25.1	0.49	−2.7	68.4	80	Medium
Dichogaster spp. (polyhumic endogeics)	Australia	Grasses	10	24.4	0.25	+46.5	321.4	70	High
Drawida willsii (epianecic)	India	Rice	6	23.8	0.71	+55.9	483.8	100	High
Eisenia rosea (mesohumic endogeic)	Australia	Oats	4	22.5	0.57	−134.8	1.2	75	Low
Amynthas spp. (polyhumic endogeics)	Australia, Brazil	Grasses, *Mimosa*	13	19.2	0.26	−18.4	68.4	84	Medium
Millsonia anomala + Eudrilidae[e]	Ivory Coast	Maize	3	13.5	0.70	−6.0	89.4	100	Medium
Eudrilus eugeniae (polyhumic endogeic)	Australia	Grasses	9	12.9	0.62	−77.3	35.5	66	Low
Drawida barwelli	Australia	Grasses	4	12.8	0.72	+4.8	113.7	75	Medium
Polypheretima taprobanae (mesohumic endogeic)	Australia	Grasses	5	11.2	0.64	−26.9	80.3	80	Medium
Aporrectodea trapezoides (mesohumic endogeic)	Australia	Sorghum, grasses	7	9.6	0.81	−48.4	93.4	100	Medium
Hyperiodrilus africanus (polyhumic endogeic)	Ivory Coast		4	6.9	0.97	−46.7	14.5	50	Low

Table 4.6. *Continued*

Earthworm species (ecological category)	Location	Crops most affected[a]	n[b]	Shoot increase (%)	*P* value	Change in mass (g m^{-2})	Mean survival (%)	Positive results (%)	Potential (see text)
Pontoscolex corethrurus + *Polypheretima elongata*	Mexico	Maize	12	5.9	0.89	?	n.d.	80	Low
Fletcherodrilus unicus	Australia		4	4.2	0.91	−140.6	23.2	75	Low
Diplotrema sp. nov. 2	Australia		2	3.6	0.94	+20.1	183.2	100	Medium
Metaphire californica (epigeic?)	Australia		4	3.2	0.98	−25.6	80	75	Medium
Perionyx excavatus (epigeic)	Australia		1	−1.2	–	−12.0	61.5	0	Low
Eukerria saltensis (polyhumic endogeic)	Australia		4	−2.4	0.89	+0.2	101.7	25	Low
Octochaetus beatrix	Australia	Oats	4	−3.5	0.84	−38.1	40.0	50	Low
Ocnerodrilus occidentalis + others[f] (polyhumic endogeics)	Australia		1	−11.6	–	−9.4	60.0	0	Low
Digaster brunneus	Australia		2	−12.2	0.81	−111.6	0	0	Low
Spenceriella minor	Australia		2	−22.5	0.60	−35.0	22.7	0	Low

[a] Crops are mentioned only when increase is > 10%.
[b] *n* = number of observations.
[c] Other species added in low quantities were *Notoscolex* sp., *Metaphire houlleti*, *Megascolex konkanensis* and *Amynthas corticis*.
[d] This is a special case; see text for explanation.
[e] Other species added were *C. zielae* and *S. porifera*.
[f] Other species added were *Gordiogrilus elegans* and *Dichogaster bolaui*.

Amynthas sp. additions to tea in India) were significant earthworm effects detected. This does not mean, however, that a given species of earthworm did not increase shoot production in individual experiments. In fact, this was often the case, so the potential of each species for introduction and/or management in tropical and subtropical soils was assessed based on: (i) earthworm survival rates and (ii) ability to increase plant growth above a certain percentage in a given number of cases. High potential was ascribed to a species when the population biomass was maintained at > 98% of the biomass applied, and when the species promoted shoot yield increases > 20% in > 80% of the cases. Moderate potential was applied when the species population was maintained over 64%, yet promoted plant growth on average less than 20% or > 20% but in less than 60% of the cases. Low potential was given when small or negative effects on biomass were obtained, or when survival of the introduced species was poor.

Earthworm addition treatments that most increased biomass, and that also had a high potential for use in tropical soils, were those including the species *P. corethrurus*. Under tea cropping in India, this species together with four other species resulted in an increase of 217% in green leaf production (Table 4.6). When applied alone with a range of different plants in five countries, the average increase was 82%. The other six species which also showed high potential for management were *Chuniodrilus zielae* and *Stuhlmannia porifera* (69% increase) and *Millsonia anomala* (56%) at Lamto, *Dichogaster affinis* and *Dichogaster saliens* (24%) in Australia and *Drawida willsii* (24%) in India. Treatments with *Heteroporodrilus bongeen* and the combination of *Drawida barwelli* and *Amynthas minimus*, also in Australia, led to important biomass increases, but the earthworm populations added were not sustainable; these species thus showed low potential for management. Many species that had medium potentials, including five native and locally distributed species (*M. anomala* + *C. zielae* and *S. porifera*, *Diplotrema* sp. nov. 1 and *Diplotrema* sp. nov. 2) and eight widespread exotic peregrine species, could easily be of high value if managed properly, for example with appropriate plant species and soil types.

Interestingly, in several cases, the addition of more than one species of earthworms increased plant production more than the addition of each species separately (e.g. *A. trapezoides* + *E. rosea*, *D. barwelli* + *A. minimus*, *P. corethrurus* + others). Thus, species diversity within the soil should be taken into account, and promoted if possible, to achieve effective plant production enhancement. It is likely that, by producing a variety of structures and using different ecological niches within the soil, combinations of species are more efficient at stimulating both nutrient cycling and the conservation of a good soil structure (Chapters 5 and 6).

Average survival rates of earthworms inoculated into both pot and field experiments varied widely, depending on their ability to adapt to particular soil conditions. In the field, most of the species displayed poor survival rates, the only species surviving well and reproducing being *D. willsii* (sevenfold increase), *Amynthas* spp. (109% of inital mass added) and *P. corethrurus* (107% of initial). *M. anomala* biomass decreased to 58% of that applied. Poor earthworm survival was due to harsh climatic conditions (drought at Narayen and Samford), competition with other species (La Mancha) or the inability of the soils to support the biomasses introduced (Martinique, Ivory Coast and India). In the pot experiments, under more controlled conditions, survival rates were much higher and 15 species maintained their biomass above or close to 100% of the initial mass added, often reproducing successfully (Appendix 4.1). In particular, *P. corethrurus*, *Dichogaster affinis* and *D. saliens* displayed large increases in biomass, from four- to sixfold on average. Finding and maintaining the proper soil conditions (e.g. texture, C content, residues, pH, temperature, moisture) for each earthworm species is, therefore, essential if they are to be introduced, especially in field conditions. Earthworm biomass additions (properly chosen and tested previously for adaptibility) should not exceed that which is sustainable for the particular soil or plant conditions in question. Probably the most important practice is to ensure adequate food (C sources) availability for the earthworms (Lavelle, 1997; Chapter 6). Residues have been added with some success in Peru, Mexico and India, which, in addition to helping maintain earthworm biomass, can also increase crop yields (Pashanasi *et al.*, 1994, 1996; Giri, 1995; Patrón *et al.*, unpublished data).

Effect on different parts of the plant

Using all data available for each plant part, no significant earthworm effects between the parts were found (Table 4.3). However, if the values for the percentage increase of the tree *B. orellana* were removed from the data set (on the basis of being outliers from the rest of the data), the overall increase in shoot, root and total plant production became 42.1, 28.2 and 29.4%, respectively, while grain production increase remained unchanged (35.8%). The difference between the percentage increase of shoot and root biomass now becomes significant at $P < 0.09$. Therefore, considering all the other remaining crops, the average increase was higher for shoot than root biomass, as observed in several of the individual studies (Spain *et al.*, 1992; Pashanasi *et al.*, 1996; Derouard *et al.*, 1997). For example, when *P. corethrurus* was introduced into an Ultisol in Yurimaguas, grain and stover production over six cropping cycles averaged 46 and 34% higher, respectively, than where worms were not introduced, the equivalent of a production gain in harvested biomass of 2.1 and 2.9 Mg ha^{-1}. On the other hand, root biomass harvested at the end of each cropping cycle averaged only 23% higher in the presence of earthworms (equivalent to +0.3 Mg ha^{-1}). Although the harvesting procedure did not include intermediate harvests to estimate root growth over the cropping cycle, and no estimates of root turnover were made, this phenomenon may still pose potential hazards to OM sustainability within the soil, particularly if the grain and stover are removed from the system and root biomass is the main OM input remaining. Over time, this could lead to a decrease in OM inputs into the soil due to earthworm activities, resulting in an overall loss of organic C as well as other nutrients found in plant matter, such as N and P, from the soil (Gilot 1994, Chapter 6; Charpentier, 1996). However, if a reasonable portion of the stover is maintained, this potential loss could be arrested.

Table 4.7 summarizes the results on the percentage increase of different plant parts due to earthworm activity (irrespective of earthworm species), as well as the proportion of positive results (increases) obtained for 12 plants. The data clearly demonstrate that for plants such as maize, beans, *P. maximum* and two other grasses, cowpea and peanuts, the above-ground parts received a greater stimulation than roots due to earthworm activities. Since the harvesting of the first four plants involves the removal of above-ground parts, and the latter plant is below-ground harvested (peanuts), special attention must be paid to managing the soil organic matter (SOM) pool, to prevent potential soil C losses induced by earthworm activities. In contrast, root biomass of rice and all four tree plants (*B. gasipaes*, *B. orellana*, tea and *E. stipitata*) was slightly stimulated by earthworm activities. The reason for the stimulation of rice root

Table 4.7. Average percentage of positive results (increases) and percentage increase in shoot, root and grain biomass of 13 plant species (for which all three parts were available).

Plant	*n*	Increase shoot (%)	% Positive	Increase root (%)	% Positive	Increase grain (%)	% Positive
Maize[c]	17	12.6[b]	80	12.6[b]	48	42.0[a]	84
Rice	18	34.9*	78	59.7*	77	55.2	78
Sorghum	5	14.5	83	—	—	58.8*	100
P. maximum [a]	24	10.5	79	−0.9	50	—	—
P. maximum	7[b]	129.2*	86	107.6*	100	—	—
Peanuts	4	3.6	75	−5.3	25	−20.3*	0
Beans[c]	2	103.4[a]*	100	61.4[a]*	100	13.8[b]	100
Cowpea	3	16.9	66	−14.3	0	−4.9	33
Tea	8[b]	25.0*	100	53.0*	75	—	—
B. orellana	5	760.7***	100	900.2***	100	—	—
E. stipitata	5	117.4	100	164.3	80	—	—
B. gasipaes	5	−28.1	40	−22.0	20	—	—

[a] The other two species harvested were *Chloris gayana* and *Cenchrus ciliaris*.

[b] Includes only data from the potted plants.

[c] Values with the same letters are not significantly different at $P < 0.05$ (maize and beans).

Statistical significance for earthworm effects as in Fig. 4.3.

biomass is not known and should be investigated further. The other four plants are perennial dicotyledenous species, with life cycles, root growth and nutrient requirements different from those of the previously mentioned crops, factors which may have affected the ability of the earthworms (*P. corethrurus*, primarily) to stimulate root growth. As mentioned earlier, *P. corethrurus* does not favour overall growth of *B. gasipaes*. Both shoot and root biomass of this plant were reduced by the presence of the earthworm.

The enhancement of shoot/root ratios by earthworm activity in several of the crops mentioned above supports the hypothesis that plants invest more energy in above-ground (especially fruit or grain) growth because plants are healthier and able to absorb more essential elements and water from soils colonized by earthworms. Spain *et al.* (1992) found higher N and P uptake by *P. maximum* shoots and roots in the presence of several earthworm species, and Gilot *et al.* (1996) found that *M. anomala* activities enhanced ^{15}N uptake from decomposing plant residues incorporated into the soil. On the other hand, at Yurimaguas, no differences in nutrient uptake by the different crops were found over six cropping cycles (Pashanasi *et al.*, 1996). Nevertheless, plant tissue analyses should always be performed to reveal the stocks of nutrients taken up by the plants and to assess the potential need for fertilization or OM addition to maintain soil fertility. Such additions should be related to the increased uptake and export of nutrients from the soil system due to earthworm activies, especially N and P (Blakemore, 1994; Charpentier, 1996) harvested in the above-ground biomass (grain and/or shoot).

Mechanisms involved

Earthworm activities modify many soil properties which affect plant growth rates and, ultimately, crop yields. These range from large-scale effects such as acceleration of soil profile formation (e.g. mollic and vermic A horizons) to enhancement of soil microbial activities (e.g. respiration, production of plant growth regulators, antibiotics) at the microscopic level (Brown, 1995). A major problem, however, has been determining which soil, plant or earthworm characteristics are the most important mechanism for the observed effects in a given situtation. The drilosphere, i.e. the soil fraction modified by earthworm activities (Lavelle, 1988), including casts, burrow systems and gut processes, is generally very different from soil unmodified by the worms (Brown, 1995), and its extent and characteristics (e.g. fertility, physical properties) depend on earthworm species and ecological category together with soil and climatic conditions (Chapters 3 and 5).

The factors and processes of the drilosphere and the ways in which they influence plant growth (especially roots) are summarized in Fig. 4.5. The changes important to soil fertility and plant production begin when the earthworm ingests the soil, selectively choosing particular particle sizes or regions rich in OM or with high microbial activity, and these are subjected to various

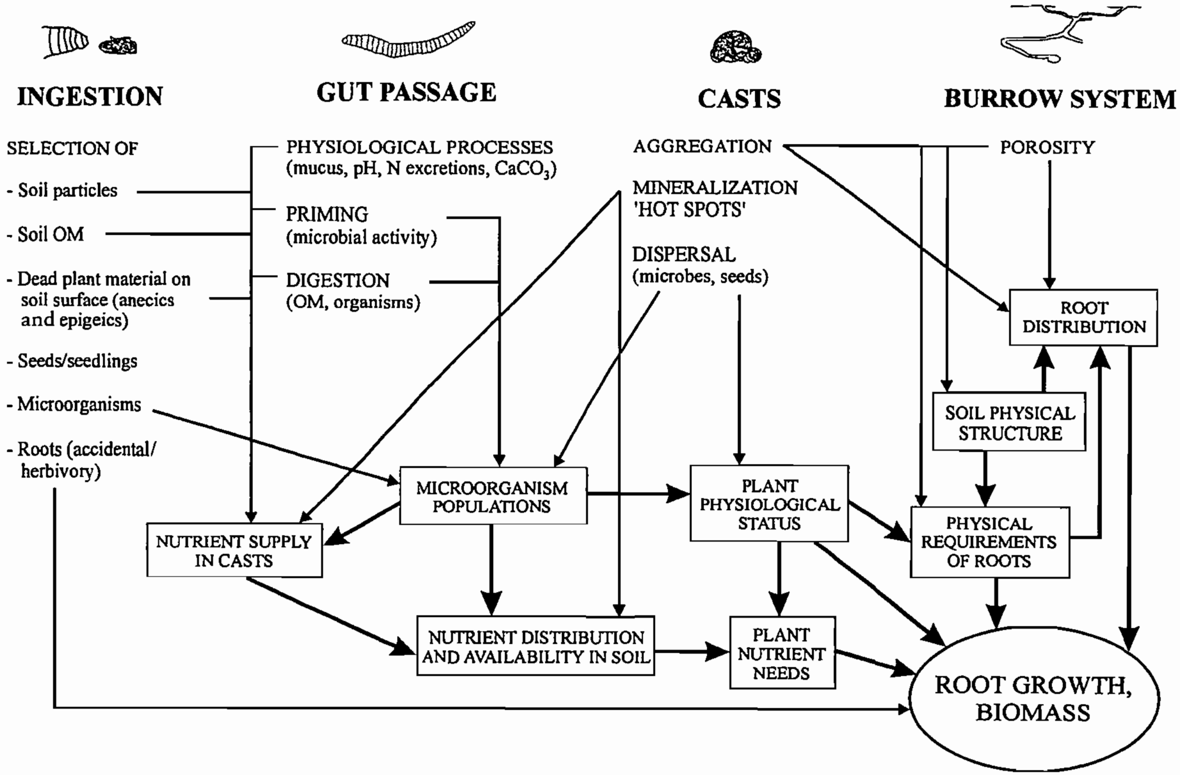

Fig. 4.5. Mechanisms by which the drilosphere properties (earthworm casts, burrows, gut) and its associated processes influence plant growth (especially roots).

transformations as they pass through the earthworm gut. These processes (ingestion and gut passage) determine the richness of the egested castings, which are characterized by higher available nutrient contents and microorganism populations (Chapter 3). Beneficial or antagonistic organisms as well as plant seeds may also be dispersed throughout the soil by earthworm activities. The combination of aggregates produced (castings) within the soil and the burrows dug through the profile determine the physical structure of the soil, influencing its capacity to hold air and water, and to permit adequate root growth. The sum of these phenomena thus determines the overall effect of a worm community on potential plant response, depending on the worm species (and ecological category) composition and the particular requirements of the plant community.

The Macrofauna programme has contributed greatly to the understanding of many mechanisms of plant growth changes (both positive and negative) due to earthworm activities. These can be divided into three general categories, i.e. chemical, physical and biological.

1. Biological factors affecting earthworm-induced changes in plant biomass include:

- differential responses of specific plant parts, especially above-ground portions;
- markedly different effects depending on plant and earthworm species used in combination;
- earthworm biomass (see later discussion);
- competition between earthworms and plants for water;
- the extent of rhizosphere and bulk soil feeding activities;
- preference of different earthworm species for particular plant rhizospheres;
- changes in (increased or reduced) microbial biomass and priming of microbial activity in the gut and casts;
- release of enzymes by microorganisms and earthworms in the gut, leading to changes in C and nutrient status of ingested food and casts;
- increased dispersal and promotion of root infection by vesicular–arbuscular mycorrhizal (VAM) fungi (Fig. 4.6) and ectomycorrhizal fungi, in appropriate plants;
- reduced damage from plant parasitic nematodes (Fig. 4.7);
- increased nutrient uptake by plants;

(Pashanasi *et al.*, 1992, 1994, 1996; Gilot, 1994; Lavelle and Gilot, 1994; Ydrogo, 1994; Giri, 1995; Derouard *et al.*, 1997; Boyer, 1998; Lattaud *et al.*, 1998; Brown *et al.*, unpublished data; Brussaard *et al.*, unpublished data; Charpentier *et al.*, unpublished data; Patrón *et al.*, unpublished data;).

2. Among the chemical factors observed were increased nutrient (especially N, P, K; a few micronutrients) availabilities in casts and burrows due to microbial activation or earthworm-induced changes in nutrient solubility; selection

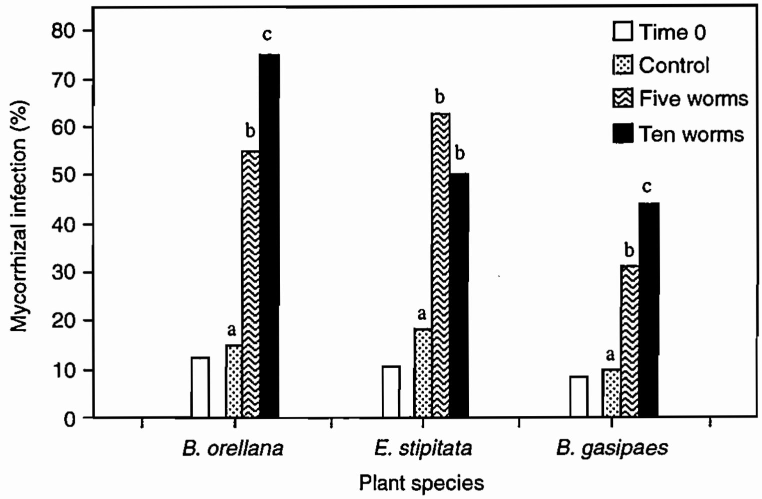

Fig. 4.6. Mycorrhizal infection in roots after various durations of greenhouse culture of tree seedling species *Bixa orellana* (120 days), *Eugenia stipitata* (240 days) and *Bactris gasipaes* (210 days) in the absence of earthworms (control), or in the presence of five (0.375 g) and ten (0.75 g) *P. corethrurus* in Yurimaguas, Peru (Ydrogo, 1994). Bars with different letters indicate significant differences at $P < 0.05$.

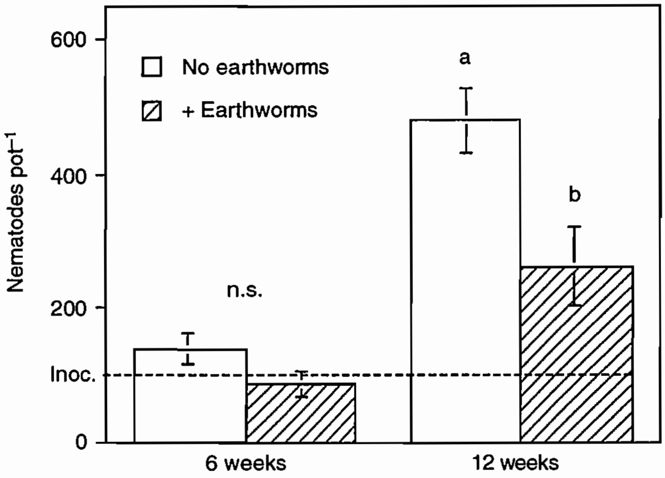

Fig. 4.7. Number of plant parasitic nematodes (*Pratylenchus zeae*) recovered per pot after one and two generation times (6 and 12 weeks) in small pots planted with rice with and without *P. corethrurus* (Boyer, 1998). n.s. = differences not significant; different letters indicate significant differences at $P < 0.01$. Initial inoculum density = 100 nematodes per pot.

of richer soil portions by the earthworms; addition of nutrients from dead worm tissues, mucus and other excretions; and accelerated nutrient release from decomposing plant residues (Chapter 3; Lavelle *et al.*, 1992; López-Hernández *et al.*, 1993; Chapuis 1994; Gilot, 1994; Chapuis and Brossard, 1995; Brossard *et al.*, 1996; Brussaard *et al.*, unpublished data; Pashanasi *et al.*, 1994; 1996).

3. Physical factors included amelioration of soil physical properties limiting plant growth under certain conditions leading to an increased proportion of water-stable macroaggregates, changes in porosity, aeration and water infiltration, an increase or decrease in bulk density and crusting, and the creation of burrows which act as preferential pathways for plant root growth (Chapter 5; Gilot, 1994; Pashanasi *et al.*, 1994, 1996; Giri, 1995; Derouard *et al.*, 1997; Brussaard *et al.*, unpublished data; Patrón *et al.*, unpublished data).

Other mechanisms have also been associated with plant growth enhancement due to earthworm activity (see Fig. 4.5). These have been shown mostly for lumbricid earthworm species and are primarily biological or biochemical in nature. They include:

1. Dispersal and enhancement of plant growth-promoting rhizobacteria (PGPR) such as *Enterobacter cloacae, Acinetobacter, Azotobacter, Azospirillum, Pseudomonas* and *Bacillus* spp. in the casts and drilosphere (Bhat *et al.*, 1960; Kozlovskaya and Zhdannikova, 1961; Kozlovskaya and Zaguralskaya, 1966; Bhatnagar, 1975; Loquet *et al.*, 1977; Hand and Hayes, 1983; Pederson and Hendriksen, 1993), and the promotion of plant growth regulator (auxins, cytokinins, gibberellins and ethylene) production by microorganisms in the casts (Krishnamoorthy and Vajranabhaiah, 1986; Tomati *et al.*, 1988; Simek and Pizl, 1989; Nardi *et al.*, 1994; Tomati and Galli, 1995), which may dramatically alter plant growth and architecture.

2. Stimulation of enzyme production (e.g. phosphatases, nitrogenase, urease) by cast- and burrow-inhabiting microorganisms (Loquet *et al.*, 1977; Satchell and Martin, 1984; Syers and Springett, 1984; Mulongoy and Bedoret, 1989; Simek and Pizl, 1989; Zou, 1992).

3. Spread and enhancement of *Rhizobia* and N_2 fixation in leguminous plants (Rouelle, 1983; Thompson *et al.*, 1993; Doube *et al.*, 1994a; Stephens *et al.*, 1994c) and spread of actinomycetes such as *Frankia* spp. in earthworm casts resulting in increased infection (nodule formation) in susceptible plants (such as *Casuarina equisetifolia*; Reddell and Spain, 1991b), as well as the addition of N to the drilosphere through associative (non-symbiotic) N_2 fixation by microorganisms such as *Chlostridia* spp. in the earthworm gut (Barois *et al.*, 1987; Striganova *et al.*, 1989).

4. Dispersal of biocontrol agents (e.g. *Pseudomonas corrugata)* which reduce plant disease (Stephens *et al.*, 1993; Doube *et al.*, 1994b), or direct reduction of plant root diseases such as the fungi *Rhizoctonia solani* (the causative agent of '*Rhizoctonia* bare patch' disease) and *Gaeumannomyces graminis* var. *tritici* (the causal agent of take-all disease) by *Aporrectodea* spp. (Stephens *et al.*, 1994a;

Stephens and Davoren, 1995), and the reduction in infectivity of cowpea and tobacco mosaic viruses by earthworm (*Eisenia fetida*) enzyme extracts (Amaravadi *et al.*, 1990).

5. Ingestion and/or burial of leaves, causing reduction in populations of surface litter-inhabiting pathogenic fungi (Niklas and Kennel, 1981; Kennel, 1990), including *Venturia inaequalis* (causal agent of apple scab) by litter-feeding earthworm species such as *Lumbricus terrestris.*

6. Seed consumption and/or burial, leading to the preferential germination of some plant species' seeds (Grant, 1983; van der Reest and Rogaar, 1988; Thompson *et al.*, 1993, 1994; Piearce *et al.*, 1994, Shumway and Koide, 1994).

7. Dead or live root consumption (Carpenter, 1985) and feeding on germinating plant seedlings (Shumway and Koide, 1994) by lumbricid earthworms.

8 An increase in nitrate reductase activity and protein synthesis leading to a more efficient photosynthesis by plants (Galli *et al.*, 1990; Tomati *et al.*, 1990; 1996; Tomati and Galli, 1995).

It is important to note that not all of the forementioned mechanisms act on the soil and the plant at one time. These mechanisms are complex and dependent on the crop–soil–worm combinations. Thus it is unlikely that the same suite of mechanisms will be applicable in two different locations, even for the same crop and earthworm species. Earthworms modify soil properties at large and small spatiotemporal scales. Over the short term, a cropping cycle for example, modification of soil in or near the rhizosphere is likely to lead to significant earthworm effects on plant growth. If nutrients or physical conditions are limiting plant growth to some extent, and earthworms help to reduce these limiting factors, plants will respond positively. Thus, at the rhizosphere level, quantification of earthworm activity on both the physical (spatial) and biochemical scales is essential if we are to assess what impact earthworms have on crop root growth and hence on above-ground yields.

Several approaches have been made to the question of spatial synchrony of earthworm activities with plant rhizospheres, and some progress has been made in this area. ^{13}C analysis of *P. corethrurus* (a polyhumic endogeic which lives primarily in the top 10 cm of the soil—essentially the zone of highest root density) tissue in sugar-cane plantations (Spain *et al.*, 1990) and under maize (Brown, 1999) suggests that this earthworm feeds at least partly on C derived from the rhizosphere of these crops. On the other hand, under beans, this same species and *P. elongata* do not seem to concentrate in the rhizosphere of benefit from their exudates (Brown, 1999). Furthermore, under maize, *P. elongata* also did not show preferential consumption and assimilation (using ^{15}N as a tracer) of root-derived materials (Brown, 1999). Carpenter (1985) observed lumbricid earthworms feeding on living roots in a rhizotron, in the only known case of direct visual observation of this phenomenon. Doube and Brown (1998) show photographic evidence of wheat rhizosphere feeding by *Aporrectodea trapezoides.* In a field study over 1 year using ^{32}P as a tracer, Baylis *et al.* (1986), found that three species of lumbricid earthworms actively fed on clover roots, while two other species did not. Another species, *L. terrestris* was shown to feed on both rhizosphere microorganisms and ryegrass roots, using ^{14}C as a tracer (Cortez and Bouché, 1992), and Shumway and Koide (1994) discovered partially consumed plant seedlings in the bottom of *L. terrestris* burrows.

The possibility of rhizophagous behaviour has been associated with the analysis of earthworm gizzard or gut contents for ingested root fragments. Proving active rhizophagy with this method is difficult since the organic residues are usually already partly decomposed and hard to identify when removed, and some species may ingest root fragments randomly. Nonetheless, when abundance ranking of ingested materials is performed, high proportions of roots can evidence activity in plant rhizospheres. Over 30 species have been subjected to these analyses, and the results indicate presence of root fragments in slightly more than half of the species (Table 4.8). However, in most cases, roots were a minor component of the biomass of gut contents; soil and OM of other sources were normally dominant. Both absence and presence were detected for three species (*A. caliginosa*, *A. rosea* and *A. longa*), indicating that in different environments they may be feeding on different resources, excluding or including roots, depending on the quality and quantity of available food. For example, in the savanna region of Lamto, Lavelle *et al.* (1989) showed that roots of the predominant grass species (*Loudetia simplex*) were a poor food resource for *M. anomala*, and other organic sources (leaves, SOM and dead OM) were generally preferred and ingested in greater quantities (Ka Kayondo, 1984), as well as being more effectively assimilated and earthworm growth-promoting.

Finally, not only must earthworm activities be effective at the rhizosphere level, they should also coincide both spatially and temporally with the demands for root expansion and nutrient uptake. So far, few studies have been performed addressing the temporal synchrony of earthworm activities with plant nutrient needs. These have revealed an improved uptake of ^{15}N by maize from labelled maize residues incorporated into the soil (Gilot *et al.*, 1996), and by *P. maximum* shoots from labelled soil (Spain *et al.*, 1992) in the presence of *M. anomala* over a short time (< 90 days). Brown *et al.* (unpublished data) observed an important effect of *P. corethrurus* and *P. elongata* on maize and bean root distribution and density, leading to greater bean biomass, but no significant difference in maize production. Further experimentation in this field is required to clarify the extent of synchrony between earthworm effects on soil properties and the physical and chemical needs of plants.

The above results led us to conclude that several earthworm species may be active in the rhizosphere of at least some plant species, and that they may be grazing on dead or live roots (though the latter is less likely), or on rhizosphere exudates, assimilable organic matter or microorganisms (protozoa, fungi, bacteria, nematodes) (Brown, 1995, 1999). In addition, earthworms may be important in mycorrhizal (both ecto and endo) fungi dispersal and the

Table 4.8. Presence and absence of root fragments in the intestinal contents of several earthworm species from tropical and temperate regions.

Root fragments	Earthworm species	Reference
Present	*Aporrectodea rosea, A. chlorotica, Lumbricus terrestris*	Ferrière (1980)
	Nicodrilus caliginosus, Eisenia nordenskioldi	Striganova (1982, 1984)
	L. rubellus, A. caliginosa, A. chlorotica, Aporrectodea longa	(Piearce, 1978)
	P. corethrurus	Reddell and Spain (1991a)
	Millsonia lamtoiana, Dichogaster terrae-nigrae	Ka Kayondo (1984)
	Digaster sp., *Heteroporodrilus* spp.	Blakemore (1994)
	Anteoides sp.	Németh (1981)
	Diplocardia longiseta, D. smithii, D. rugosa, D. prosenteris, D. verrucosa, A. turgida, Octalasion cyaneum	James and Cunningham (1988)
Absent	*Dendrobaena mammalis, Lumbricus castaneus*	Piearce (1978)
	L. castaneus, Nicodrilus longus ripicola, N. longus longus, N. caliginosus, A. icterica, N. nocturnus, D. mammalis	Ferrière (1980)
	Aporrectodea rosea	Judas (1992), Bouché and Kretzschmar (1974)
	M. anomala	Lavelle (1971)
	Several tropical species	Lavelle (1978, personal observation)
	Andiorrhinus amazonius, Andiorrhinus sp. 1, sp. 2	Németh (1981)

infection potential in host plants (Reddell and Spain, 1991a; Ydrogo, 1994; Brown, 1995). Given the importance of these fungi in enhancing plant nutrient uptake in poor soils and the fact that as much as 90% of all plants are mycorrhizal symbionts, there is potential for exploring the roles of earthworms in these processes, especially in tropical forestry (in relation to Casuarinales, *Eucalyptus* and *Pinus* spp.) and in cultivated soils, where inoculum potential is generally low.

Earthworm abundance and biomass vs. plant response (dose–effect) relationships

The fact that earthworms may be important in plant production is by now clearly evident. However, the question of how many, and what biomass is necessary for earthworms to become important remains. The first reports by Hopp (1954) suggested that a minimum of approximately 100 earthworms m^{-2} were necessary to be important in the physical conditioning of soil (and thus in affecting crop growth). In New Zealand, Waters (1951) found a significant correlation ($r = 0.87$) between pasture dry matter production and earthworm biomass; however, it appears that the chief agents in raising the yield in pastures with earthworms were the presence of clover and nutrient additions (dung and urine), which also raised the earthworm biomass.

Only recently have such biomass–yield relationships been established for tropical earthworm species. In Papua New Guinea, Rose and Wood (1980) found a relationship between sweet potato topgrowth and earthworm (> 99% *P. corethrurus*) biomass in potato mounds. When the biomass was < 43 g m^{-2}, the relationship with shoot weight was positive ($r = 0.48$, $P < 0.01$); above 43 g m^{-2}, this relationship was lost. The correlation also varied depending on soil type and plant part; in an alluvial soil (sandier), a positive correlation ($r = 0.6$) with topgrowth was found, but in a clayey peat soil, worm biomass was negatively correlated ($r = -0.61$) with tuber production.

At Lamto, Spain *et al.* (1992), found a significant correlation ($r = 0.81$; $P < 0.01$) between total dry matter produced by maize and the biomass of *M. anomala* and Eudrilidae earthworms found at the end of the experiment. They also found that increasing application of *M. anomala* biomass increased *P. maximum* yields up to a point, whereafter the effect was reduced, suggesting a curvilinear (polynomial) relationship ($r = 0.96$). In this case, biomass applied above 100 g m^{-2} caused a reduction in growth stimulation, attributed to compaction from the excess soil working by these earthworms (Blanchart *et al.*, 1989, 1990). Nevertheless, if final biomass of *M. anomala* obtained at harvest was associated with the same *P. maximum* shoot biomass used above, the relationship became exponential ($r = 0.97$).

In a tropical pasture in Sambalpur, India, with a predominance (> 80% of biomass) of the grass species *Eragrostis amabilis*, *Cynodon* sp. and *C. dactylon*, Senapati and Dash (1981) established a significant positive relationship ($r = 0.78$) between mean monthly earthworm biomass (five species, dominance of *Octochaetona surensis*) and above-ground plant biomass for both grazed and ungrazed plots. Root biomass was positively correlated with earthworm biomass only in the ungrazed plot ($r = 0.38$). Both earthworm and shoot biomass followed a similar monthly cycle throughout the year, both being correlated with and depending on primarily soil moisture (positively) and temperature (negatively).

In a native pasture (*Sporobolus jacquemonti*, *Paspalum notatum* and *Setaria* sp. predominant) at La Vibora, Mexico, monthly sampling of approximately six earthworm species (dominated by an undescribed Glossoscolecidae sp.) and green and dry grass during 10 months of a year revealed significant ($P < 0.001$) positive correlations ($r = 0.52$) of annual (yearly total) earthworm biomass and numbers with green grass yields (Brown *et al.*, 1998). Nevertheless, both earthworm and plant factors were significantly correlated with soil moisture (a main factor limiting both plant production and earthworms for at least 6 months of the year), confounding the relationship between the two. Nevertheless, when peak earthworm biomass and numbers (September) were present, and the average pasture production was high, the relationship between green production and earthworm populations was significant ($r = 0.4$, $P < 0.05$), while production was not related to soil moisture. This showed that earthworms had the potential to concentrate in the regions of higher plant production, in a synergistic association, in which the plants can benefit from worm activity in the rhizosphere and from the higher nutrient contents in the drilosphere, and the earthworm benefit from higher OM inputs in shoot litter, roots and rhizosphere deposition.

Using data from field trials at Yurimaguas, Lamto and La Mancha, Lavelle (1997) developed a relationship between earthworm biomass and percentage increase of grain yield ($r = 0.53$, $P < 0.05$). The important increases in yield were obtained mostly when earthworm biomass was above about 30 g m^{-2}.

Using all the data obtained from pot and field experiments performed during the Macrofauna programme and from the literature for tropical regions, several regression analyses were performed, using root, shoot and grain biomass increase and earthworm biomass applied and recovered at the end of each trial. No significant relationship between earthworm biomass and shoot and root biomass was found. However, when only the grain percentage increase data (for cowpea, beans, rice, maize, sorghum, wheat) were correlated with the difference in earthworm biomass between inoculated and uninoculated treatments, a small but significant linear relationship was found ($r = 0.31$, $P < 0.015$) (Fig. 4.8). Moderate (20–40%) and agriculturally important (> 40%) grain production increases were found with just over 13 and 47 g m^{-2} earthworm biomass, respectively. Using the same data, the curvilinear relationship (second order polynomial; Fig. 4.8) had slightly higher correlation ($r = 0.41$), where moderate (20–40%) and important (> 40%) grain production increases were found with a biomass value above 17 and 32 g m^{-2}, respectively, with maximum grain increases (~70%) at around 80 g m^{-2}. Root biomass increase of these grain crops was also positively correlated with earthworm biomass difference (linear $r = 0.39$, $P < 0.006$; curvilinear $r = 0.42$). Similarly, maximum values (55%) were found with a biomass of about 75 g m^{-2}.

In the first instance, these results appear to indicate that earthworms may positively influence grain production at biomass values that occur in some agricultural fields, or at least at a biomass achievable through soil

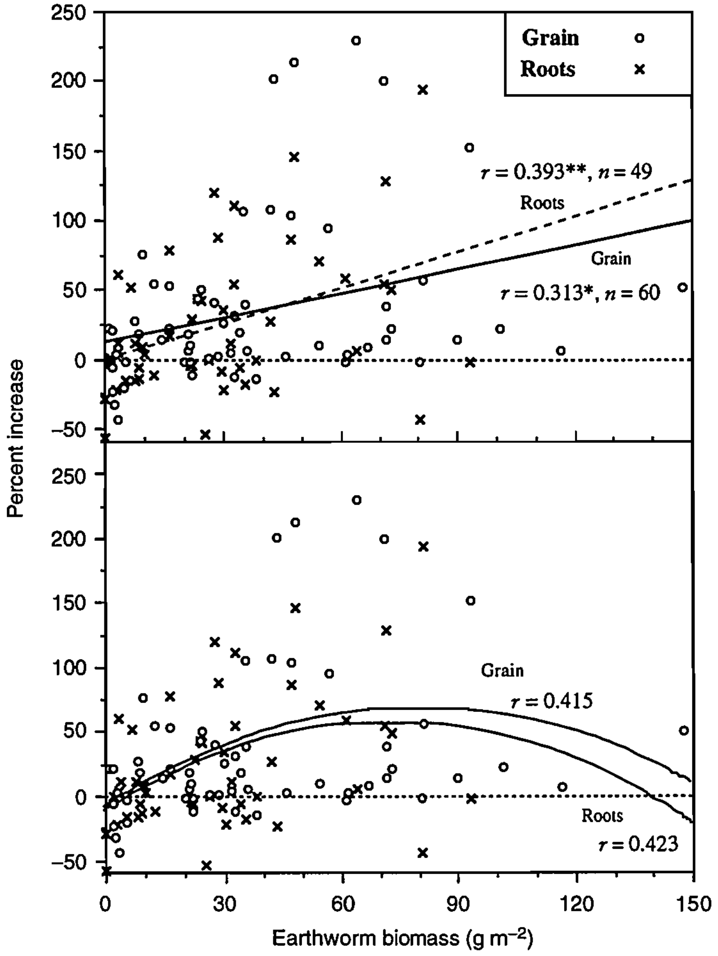

Fig. 4.8. Relationship between the increase in grain and root biomass due to the presence of earthworms and the difference in the biomass of earthworms obtained between worm addition and no-worm treatments for 60 (grain) and 49 (root) data points taken from 12 trials with six crops (maize, rice, sorghum, wheat, beans and cowpea). Significance values as in Fig. 4.3.

management techniques that stimulate earthworm populations. Secondly, however, they also bring up the question: can there be too much of a good thing? Spain *et al.* (1992) proposed that there may be a biomass beyond which the soil working activities of earthworms (particularly monospecific communities) become detrimental to plant production. The limit is most likely variable, depending on the plant and earthworm species or assemblage, soil type and the length of time earthworms have been active (the extent of the drilosphere effects on soil properties). At present, four case studies have shown negative effects on plant production of high earthworm biomass in the field. The first refers to a *Dichogaster* sp. (*D. curgensis*) as a potential pest in rice fields, but also referring to various annelids playing the same role. These earthworms are adapted to living in flooded conditions but, under particular situations, can infest rice fields reaching densities of up to > 10,000 m^{-2} (assuming average weights of ~ 0.3 g $worm^{-1}$, this equals 3000 g m^{-2}), at which point the mere fact of their movement within the soil damages the rice roots, resulting in total crop failure at densities above 7000 m^{-2} (Barrion and Litsinger, 1996). The second case was in a 15-year-old abandoned pasture (*Brachiaria* sp.) in the Brazilian Amazonia, north of Manaus, where the lack of decompacting species, and the activity of *P. corethrurus* (the only species present) with a mean biomass of 45 g m^{-2}, led to the degradation of the topsoil structure (compaction, reduced infiltration) and reduction of pasture grass growth (Barros *et al.*, 1996). The third case was found in Papua New Guinea, where sweet potato tuber yields decreased in a clayey soil where *P. corethrurus* biomass was higher than about 40 g m^{-2} (Rose and Wood, 1980). The final case was in a vegetable garden of about 1.8 ha in India, where a *P. corethrurus* population of 1308 m^{-2} in association with 247 m^{-2} *P. elongata* (equivalent to biomasses of ~520 and 240 g m^{-2}) caused severe soil compaction reducing the yields of carrots, raddish, beans and knol-khol (*Brassica oleracea*) (Puttarudriah and Shivashankara-Sastry, 1961). Interestingly, in this garden, yield reductions were observed only in dicotyledonous plants; monocot plants such as maize and ragi (*Eleusine coracana*) with a fibrous root system grew well, without an adverse effect of the high worm biomass. These cases not only confirm the probability of a biomass versus yield relationship upper limit, but also highlight the importance of promoting a diverse assemblage of earthworm species, with both soil-compacting and decompacting strategies, to arrest any possible detrimental effects of a high biomass and activity of a single species (or several species with the same strategy), e.g. the soil-compacting *P. corethrurus*.

Effects of spatio-temporal scales of investigation

Two spatial scales were investigated: field trials and pot experiments. The field trials consisted of mesocosms or small plots, and massive inoculation trials (hectare scale). Approximately half of the data on shoot, root and grain percentage increase comes from pot experiments and the other half from field experiments. When taken separately, results suggest different trends for the effects of earthworms on biomass increase of the different plant parts, depending on the spatial scale of investigation (Table 4.9). In almost every case, higher (but not always significantly different) results were obtained at the pot level for a given plant and earthworms combination. Nevertheless, *F*-tests revealed that grain and shoot production in the field trials were significantly higher in earthworm treatments than controls at lower *P*-values than in the pot trials (less variable results). Grain production was significantly higher at $P < 0.1$ and shoot biomass at $P < 0.11$. The reasons for the higher results at

Table 4.9. Mean ± SE of percentage increases of different plant parts (shoot, root, grain), due to the presence of earthworms in field trials and pot experiments.

	Field trials				Pot experiments			
Plant part	*n*	% Increase[a]	SE	*P* value[b]	*n*	% Increase	SE	*P* value[b]
Shoot	104	59.6[a]	8.5	0.11	142	54.6[a]	14.9	0.33
Grain	66	29.7[b]	10.5	0.10	23	53.3[a]	16.3	0.40
Root	35	29.8[a,b]	9.3	0.96	80	81.9[a]	31.0	0.79

[a]Values with the same letters are not significantly different at $P < 0.05$; [b]Results of the *F*-test comparing means of earthworm inoculated and uninoculated treatments for each plant part.

the pot level are likely to be related to the overall higher biomass of earthworms applied, reduced soil and environmental variability, close contact enforced between the rhizosphere and drilosphere systems, and the easier general care of the trials. Nevertheless, the greater number of species of both plants and worms used inevitably led to a greater variability of the results.

Two large-scale earthworm introduction trials were carried out as part of the second phase of the Macrofauna project. The first experiment, at Yurimaguas, was abandoned. The other experiment, still in place, in a tea plantation in India inoculated at high rates (150 kg ha^{-1} fresh wt) with *P. corethrurus* and four other species showed dramatic production increases over all the 10 months in which tea was harvested, when earthworms were introduced (Giri, 1995; Senapati *et al.*, unpublished data; Fig. 4.9). After 3 years, the positive effect on tea production is still present, although the earthworm population has not been sustained and must be reintroduced (Chapter 7). No differences were found between treatments with and without application of OM (prunings), so earthworms appear to be the main agents influencing tea production in this system.

Two temporal scales were used for the trials described in Table 4.2. The first examined the effects of earthworms over one cropping cycle, but with intermediate harvests before the final harvest at plant maturity. The second compared effects of earthworms over short-term (single cycle) and long-term (multiple cycles) experiments. The latter studies provide data on survival of earthworms over time and duration of effects on plant production (positive and/or negative), resulting in an estimate of the sustainability of earthworm introductions.

At the first level, increases in plant biomass due to earthworm activity initially were neutral or low, but increased with time such that beneficial effects were usually highest at harvest time. Furthermore, plant maturity was often more rapid in treatments that included earthworms (e.g. Pashanasi *et al.*,

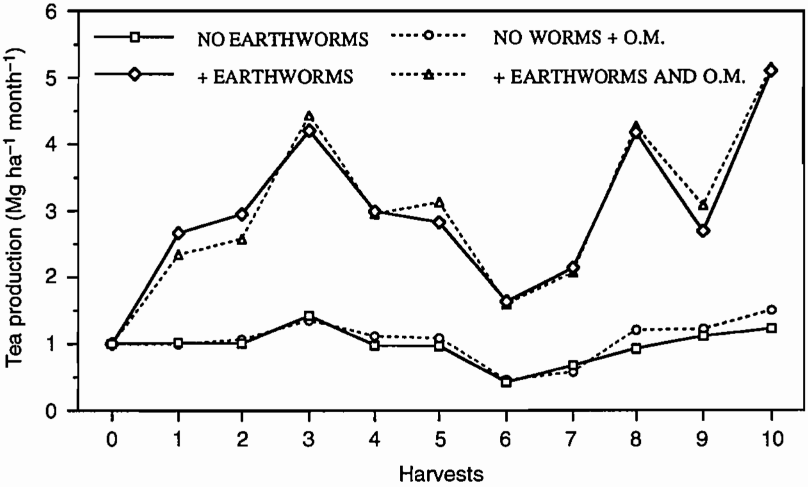

Fig. 4.9. Monthly green leaf tea production (in Mg ha^{-1}) as affected by the introduction of earthworms (primarily *P. corethrurus*) and organic matter into trenches of 0.54 m^2 at Lower Sheikamuldi Tea Estate, Parry Agro Industries Ltd, Tamil Nadu, India (Giri, 1995; Senapati *et al.*, unpublished data).

1996). This is probably due to reorganization of the soil (in trials using sieved soil), and enhanced microbial activity and nutrient release which create cumulative effects on the plant. This phenomenon was observed for three tree seedlings by Ydrogo (1994) and Pashanasi *et al.* (1992) although, for *B. gasipaes*, the latter authors found a cumulative decrease in biomass after 60 days. Brown *et al.* (unpublished data), also found increasing positive differences in shoot biomass of common beans over three harvests in the presence of *P. corethrurus* and *P. elongata*. Blakemore (1994) similarly found greater biomass increases of two grass species (*P. maximum* and *Chloris gayana*) in treatments with *D. affinis* and *D. saliens* up to 5 months, after which the growth stabilized until final harvest (8.5 months). However, when he tested the effect of 12 earthworm species in three different soil types on the growth of oats over 14 weeks (three harvests, at 42, 70 and 98 days), not only were few significant effects on biomass observed, but earthworm effects were cumulatively negative in one soil type (Narayen) for all except one worm species (*Eudrilus eugeniae*). In the other soils (Samford, Kingaroy), cumulative effects on biomass increase were mostly positive. Finally, when these same pots were seeded with two grasses (*P. maximum* and *Cenchrus ciliaris*), and harvested at 42 and 70 days, the increase in biomass was higher at the latter harvest for all earthworm species in both Narayen and Kingaroy soils. Therefore, although effects of earthworms on plant biomass increase are generally cumulative, there are situations in which they may be the reverse, depending on the soil type, earthworm and plant species.

The effects of earthworm inoculation on plant yields over several cycles were investigated at five sites (Guarapuava, Lamto, La Mancha, St Anne and Yurimaguas). At Guarapuava, both wheat and bean yields were only slightly (not significant) higher with the introduction of *Amynthas* sp. Survival of the introduced earthworms after 12 months of cropping, however, was good, averaging > 100%, indicating population increase. At Lamto, yam tuber production was significantly ($P < 0.1$) higher in two of the three cycles (Gilot, 1997) while, at both Lamto and La Mancha, few significant effects of earthworms on maize yields were observed over six continuous cropping cycles (3 years), and survival of introduced earthworms was poor (Gilot, 1994; Patrón *et al.*, unpublished data). Nevertheless, average percentage increases in grain yields were generally higher at the final three harvests at both sites, indicating that earthworms helped sustain higher production levels for a longer time period in these low-input systems. Reasons for this may be the cumulative effects of earthworm activity on nutrient and SOM dynamics, and soil biological and physical properties. At St Anne, *Digitaria decumbens* (pangola grass) root biomass, the only plant parameter measured, was not significantly influenced by the inoculation of 90 individuals m^{-2} (~ 90 g m^{-2}) of *P. elongata* throughout the experiment, and earthworm biomass was reduced due to the very low quality initial soil, although there is evidence of recovery in the last samples, probably due to soil aggradation (C increase; Blanchart, 1997). At Yurimaguas, earthworm biomass was maintained throughout six cycles, and significant positive effects of earthworm addition on crop production obtained in four of the six cycles (Fig. 4.10; Pashanasi *et al.*, 1996). In the fifth cycle, when rice was sown out of season, *P. corethrurus* caused complications in water dynamics in the soil, reducing yields (–43%). When sown in the previous and following seasons, however, rice outyielded the controls (+49 and +51%, respectively) in earthworm treatments. Despite continued cropping for 3 years and six crop cycles on the same soil, production was maintained at satisfactory levels, with slightly higher yields than crops of the same type harvested locally.

On the other hand, when maize was grown continuously over 7 years (12 cycles) in the same type of enclosures (60 cm diameter) nearby, earthworm populations were reduced (as measured by surface casting activity), and had to be reintroduced at the 10th cycle (Pashanasi *et al.*, unpublished data). Introduction of *P. corethrurus* also did not arrest the loss of soil fertility due to cropping. By the third harvest, grain production was practically nil in both treatments with and without earthworm addition. Fertilizers then had to be added for all the following eight cycles. Despite fertilization, earthworms continued to affect yields positively, although the cumulative effect was lower after the sixth harvest than over the first six harvests. By the end of the sixth cycle, the cumulative difference in grain production was as much as 5.1 Mg ha^{-1}, the equivalent of approximately two or three single harvests (Fig. 4.11). The following six harvests accumulated only 0.6 Mg ha^{-1} more, for a total of 5.7 Mg ha^{-1} above the uninoculated treatments. Thus, the effect

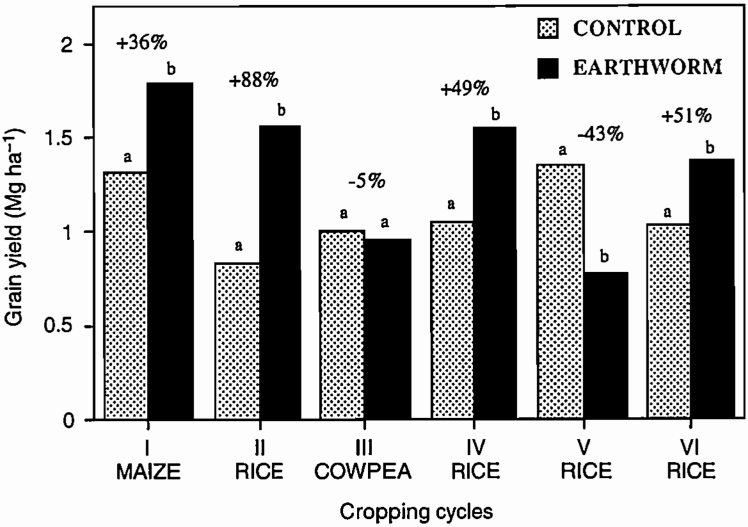

Fig. 4.10. Effect of earthworm (*P. corethrurus*) activities on grain production (in Mg ha^{-1}) in field plots of 0.28 m^2 during six successive harvests over a 3-year period, irrespective of organic treatments, at Yurimaguas, Peru (Pashanasi *et al.*, 1994, 1996). Bars with different letters indicate significant differences at $P < 0.05$.

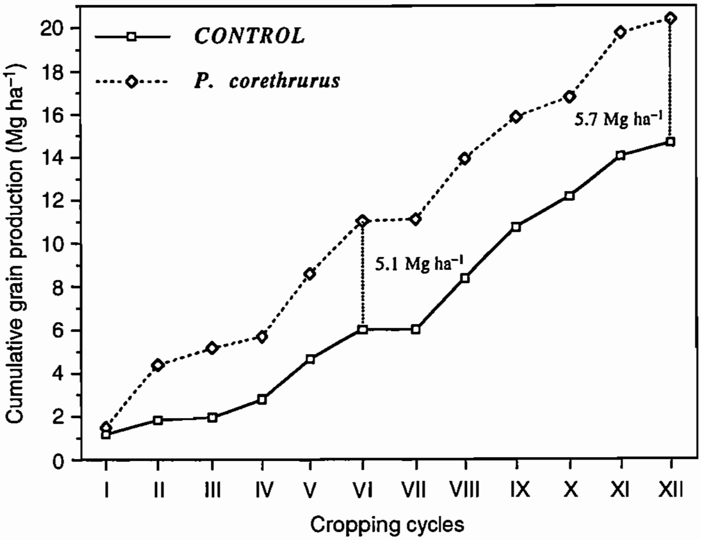

Fig. 4.11. Cumulative grain production of maize (in Mg ha^{-1}) over 7 years, including 12 cycles, in treatments with and without addition of 36 g m^{-2} of *P. corethrurus* at Yurimaguas, Peru (Charpentier, 1996; Pashanasi *et al.*, unpublished data).

of earthworms on production was positive in nine of the 12 cycles, and importantly so (> 1 Mg ha^{-1} increase) in four of the 12 cycles. However, despite this large production increase, there was evidence of greater losses of SOM due to earthworm activity at the end of the experiment (Charpentier, 1996; Chapter 6), despite the fact that in the long-term (decades), these losses may be balanced out by the conservation of C in earthworm castings versus uningested soil (Chapter 6). Therefore, attempts must be made to manage not only earthworms, but also OM (with use of residues) and cropping systems (rotations) in a holistic manner.

Limitations and future prospects

The large number of earthworm and crop species tested in tropical and temperate regions confirms the dependence of plant response on earthworm species and biomass, soil type and plant species. Additional factors such as microclimate or slight genetic differences may also be important. Field population associations of earthworms at a given site are generally adequate since they have generally adapted to the local conditions, although this may not always be the case. Given that effects can range from positive to negative when the factors are varied, we are still far from being able to propose a general combination of factors which could be applicable at many different sites.

Nevertheless, a few studies have yielded promising results that may have large-scale applicability, for example the use of *P. corethrurus* along with four other species to enhance soil fertility and tea production in degraded tea plantations in India. Despite the large investment of human labour required, the cost–benefit ratios are promising (Chapter 7). *P. corethrurus* also shows promise for use in certain tree seedling nurseries. However, the applicability of this tropical species at the global level is still uncertain, and more field experiments in different cropping systems and regions, particularly on the long-term (decades) scale, are needed to confirm the observed SOM losses at Yurimaguas (Charpentier, 1996).

Based on results at the greenhouse (pot) and field levels, *Drawida barwelli* in Australia (Blakemore, 1994) and *Drawida* spp. in India (Senapati *et al.*, 1985; unpublished data; Kale *et al.*, 1989) showed promise for introduction or management on larger scales. The latter species may be particularly useful in paddy rice-based cropping systems, since they are adapted to living under water-logged conditions for some period of time (Pani, 1986; Kale *et al.*, 1989). Trials with these species in other regions and with other plants may confirm their positive role on biomass production on a larger scale.

Several other species, such as the eudrilids *E. eugeniae* in Australia, *C. zielae* and *S. porifera*, and the megascolecid *M. anomala* in Ivory Coast, have not been tested beyond a small region; despite their high potential (Table 4.6), ways must be found to increase survival and maintain their populations in field cropping systems. Furthermore, testing of these species with other plants such as *P. maximum* or other pasture grasses at the field level may result in sustainable biomass, as well as considerable yield gains.

Finally, the small polyhumic *Dichogaster* spp. have not been tested beyond a few trials in Australia, where they showed a high potential to increase yields, yet a poor survival rate when introduced into pastures. These species are widespread throughout the tropics, in both perennial and annual cropping systems (Chapter 2), yet their role in soil fertility and plant production is practically unknown. Under rice, some species of this genus may reach a pest status, but little is known of their effects on other crops, and of other species of this genus. The effects of the widespread *Amynthas* spp. and other *Metaphire* spp. on crops and soil processes are also virtually unknown. Further research may reveal that these species have a much wider applicability and potential for management and for increasing yields. Of the latter group, *P. elongata*, a widely distributed and deep burrowing species (unlike most other candidate species), deserves further attention.

A large number of other species which inhabit tropical soils have never been tested for effects on plant growth. Given the probably 6000+ species of earthworms in the world (see Chapter 1), only 10 of which have been tested in depth, further investigations such as those by Blakemore (1994, 1997) may reveal other species useful both in tropical and temperate regions. In fact, it may be preferable in some cases to use or test locally adapted or endemic species which have by their presence demonstrated their ability to survive under local conditions of climate and soil. Great care must be taken if earthworms are transported between different countries, or even between different regions in the same country, to prevent dispersal and transmission of crop and animal diseases or pests.

Pot experiments, although limited in scope (see Blakemore and Temple-Smith, 1995), have proven to be a useful tool for screening earthworm species and crops for their potential association, and to test survival of earthworms in situations where this would be impossible on a larger scale of investigation. Nevertheless, the comparison of data between experiments is often difficult, due to differences in earthworm and crop species used, lack of detailed information in specific studies, absence of a standard methodology for addressing the question of earthworm effects on plant growth, and diverse approaches and objectives of the trials. Very often, few clear links were made between observed results and underlying mechanisms. We therefore suggest for future trials a more standardized approach and a minimum data set, which will permit comparisons of trials from different regions and provide a broader understanding of earthworm influences on plant growth and biomass. For pot experiments, this should consist of:

- pasteurization or irradiation of test soils to remove residual earthworms and their cocoons;
- statistically valid replication;
- realistic crop, earthworm and soil combinations;

- proper identification of the earthworm species;
- clear specification of the quantity of earthworms applied (based on realistic fresh field biomass, not numbers) (Dalby *et al.*, 1996), and reasons for the chosen biomass;
- full physical, chemical and biological description of soils used;
- longer time periods of investigation, preferably until plant maturity, but not longer than the time by which all soil in the pot will have been consumed by the earthworms;
- analyses of key soil properties which will be affected by earthworm activity (such as bulk density, infiltration, inorganic P and N) to reveal mechanisms of the observed effects; for chemical properties, the use of stable and radioisotopes is particularly useful;
- measurement of all plant parts and plant growth throughout the cycle, with intermediate harvests; and
- proper assessment of earthworm biomass at the end of the experiment.

From the Macrofauna and other experiments in the tropics described previously, several drawbacks arose regarding inoculation of earthworms into the field on both large and small scales. First was the difficulty and cost (money and time) of obtaining sufficient earthworm biomass to apply to the plots. A possible solution to this is mass rearing of earthworms (Chapter 7). Next, few suitable sites for field inoculations, with low or nil background earthworm populations, were found, and it was almost impossible to eliminate completely the native earthworm fauna, making it difficult to obtain and maintain control (no worm) treatments. Very often, control plots or even worm-containing plots became contaminated with introduced or resident worms. Thus, comparisons of the effects on plants between worm and no-worm treaments must take into account the biomass 'difference' between the two. In addition, earthworm exclusion treatments often conserve for a certain period of time the structures and soil properties (porosity, water infiltration, abundance and composition of macroaggregates) created by the previous earthworm community, possibly masking differences between treatments until the structures and properties were broken down. Finally, low survival of introduced species implied that specific management practices such as application of OM and the use of crop rotations were necessary to promote population stabilization and/or increase.

Field trials should be performed over several cropping cycles, on large plots, preferably > 1 m^{-2}, and special care should be taken to obtain controls without earthworms; if this is not possible, or if earthworms are applied over a resident fauna, results should be compared with biomass difference between earthworm and control plots. Earthworm abundance and biomass (and species interaction, if the case) must be assessed throughout the duration of the trial, and earthworms should not be reintroduced or the feasibility of the trial for large-scale application will be sacrificed. Biomass measurements of all appropriate plant parts must be made, and the soil well characterized at the beginning of the trial (including assessment of spatial variability) and at each harvest. These data are used to ascertain the effects of earthworms on soil physical properties and fertility, including C status in long duration trials (> 3 years), and to correlate these with observed plant responses.

Conclusions

When introduced into new systems, earthworms generally improve plant productivity, especially of above-ground parts. A survey of literature in the tropics revealed for > 34 species of earthworms and 19 plants, positive effects on above-ground biomass in 72% of the cases. In 28% of the cases, earthworms reduced plant growth, but the mechanisms are unclear. Therefore, studies on the mechanisms by which earthworms affect plant growth (both positively and negatively) are an urgent research imperative.

The effects of earthworms (even of the same species) on different crop species depend on both the environmental requirements of plants and the ability of earthworms to modify the soil environment for root growth. Earthworm effects appear particularly promising in perennial crops such as tree seedlings or pasture grasses. Monocrops are not generally beneficial to earthworm populations, and thus earthworm effects on these crops are generally less. If crop rotations are implemented, the potential for beneficial earthworm effects becomes more important.

The influences of earthworms on plant growth also depend on soil characteristics. Their effects are more important in C-poor than in C-rich soils, in sandy than loamy and clayey soils, and in moderately acid than in alkaline or highly acid soils. The mechanisms by which plant growth is affected by earthworm activity are numerous, a variety of factors often being relevant in a given situation. Mechanisms range from modification of soil function at the molecular and microscopic level (e.g. greater nutrient availability in the drilosphere, increased microbial activity in casts, enhancement of VAM fungal–root colonization, and reduction in plant parasitic nematodes), to visible soil structural changes (e.g. increased macroporosity, stable aggregates), the enhancement of specific plant parts (e.g. grain) or reduction in root diseases (particularly fungal pathogens). To obtain optimal earthworm benefits on plant production, they must be synchronized both spatially and temporally with root growth and nutrient uptake.

Increased plant shoot biomass is often associated with increased earthworm biomass, especially in pastures. Moderately positive effects on plant production can begin at biomass values > 15 g m^{-2}, while important (> 40% increase) effects appear at around 30 g m^{-2}. However, a maximum earthworm biomass for particular soil, crop, earthworm and climate combinations also appears to be present, beyond which negative effects on plant biomass may result, or earthworm populations decrease to the carrying capacity of the site.

Pot experiments should be used to screen a range of earthworm species for potential effects on plants in different soils, considering that they may have a limited applicability to field situations. A standardized methodology involving realistic earthworm, crop and soil combinations, earthworm numbers and biomass equivalent to common field values, detailed descriptions of soil modification by earthworms, and harvesting of plants preferably at maturity (unless the objective is to differentiate effects on vegetative growth, in which case harvest should take place just prior to flowering) should help to increase the comparability of these trials to the field.

Several earthworm species (particularly *P. corethrurus*) show high potential for introduction into specific plant systems (e.g. tree seedlings, pastures, tea), but further experimentation in additional cropping and plant systems is necessary to assess their role in increasing plant production on a wider geographical scale. Furthermore, given the large number of earthworm species in the tropics which have not been tested for plant growth response, it is likely that more species with useful effects will be discovered with more field work.

Finally, given the obvious benefits of earthworms to plant growth and yields, agriculturists and other ecosystem managers interested in harvesting these benefits must implement practices that favour the development of a diverse assemblage of earthworm species (and other macroinvertebrates important in regulating soil properties and processes) in their target areas. This can be achieved by applying management practices such as mulching, OM conservation, crop rotation, minimum tillage, restricted use of pesticides, incorporation of legume into pastures, as well as other practices that favour a stable and adequate earthworm biomass. If earthworms are to be introduced, care must be made to introduce several adapted species (of various ecological strategies) in sufficient but not excessive numbers (and biomass) for them to persist in new soil environments, so that favourable soil properties and positive effects on plant production can be sustained.

Acknowledgements

We thank all the persons and institutions, especially the European Union, the Instituto de Ecología, A.C., IRD, the Station Experimentale Écologique de Lamto, Perry AgroIndustries and the CSIRO, who helped make the Macrofauna and other experiments possible. We also extend our gratitude to each of the persons who graciously provided the necessary data to create the figures and tables, and to perform the statistical analyses that form an essential part of this chapter. In particular, we thank Paul Hendrix and Lijbert Brussaard for their helpful comments. Finally, a special thank you to Nakato Kidza, Ellen de Groot, Laurent Derouard, Jerome Tondoh, Laure Vilcosqui, Lydie Chapuis, Fabienne Charpentier, Hector Ydrogo and Lijbert Brussaard for providing data and figures.

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Appendix 4.1.

						Grain yield (t ha^{-1})			Shoot yield (t ha^{-1})		
Country	Location	Crop	Earthworm species	Residues (kg m^{-2})	Plot size (m^2)	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]
Ivory Coast	Lamto	Yam	*M. anomala*	0.25	0.72				0.72	0.96	33.79
Ivory Coast	Lamto	Yam	*M. anomala*	0	0.72				0.47	0.58	24.18
Ivory Coast	Lamto	Yam	*M. anomala*	0.4	0.72				0.27	0.35	30.21
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	3.52	3.45	−2.00	6.62	5.94	−10.27
Ivory Coast	Lamto	Maize	*M. anomala*	0.25	1.28	3.40	3.35	−1.38	6.71	6.84	1.94
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	1.09	1.16	5.71	1.95	2.04	4.62
Ivory Coast	Lamto	Maize	*M. anomala*	0.63	1.28	1.28	1.03	−19.51	2.25	2.07	−8.00
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	1.70	1.80	5.99	3.14	3.38	7.64
Ivory Coast	Lamto	Maize	*M. anomala*	0.31	1.28	1.67	1.98	18.22	3.03	3.09	1.98
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	1.65	1.26	−23.70	3.20	2.98	−6.88
Ivory Coast	Lamto	Maize	*M. anomala*	0.35	1.28	1.51	1.81	20.21	3.25	3.40	4.62
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	1.23	1.30	5.70	3.09	3.84	24.27
Ivory Coast	Lamto	Maize	*M. anomala*	0.5	1.28	0.94	1.24	32.50	2.87	2.91	1.39
Ivory Coast	Lamto	Maize	*M. anomala*	0	1.28	0.61	0.74	21.79	1.63	1.77	8.59
Ivory Coast	Lamto	Maize	*M. anomala*	0.34	1.28	0.55	0.66	21.43	1.41	1.64	16.31
Ivory Coast	Lamto	Maize	*M. anomala*	0.16	0.72	3.02	3.57	18.23	3.67	3.44	−6.27
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64	2.10	2.68	27.62	19	19	0
Mexico	La Mancha	Maize	*P. corethrurus*	1.12	0.64	2.23	2.45	9.87	11	12	9.09
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64				7.8	8.2	5.13
Mexico	La Mancha	Maize	*P. corethrurus*	2	0.64				9.5	9.2	−3.16
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64				2.1	2.2	4.76
Mexico	La Mancha	Maize	*P. corethrurus*	0.92	0.64				3.1	3.3	6.45
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64	2.13	2.02	−5.16	5.2	6.5	25.00
Mexico	La Mancha	Maize	*P. corethrurus*	0.33	0.64	2.00	2.05	2.50	5.7	7	22.81
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64	1.00	1.43	43.00	19	20	5.26
Mexico	La Mancha	Maize	*P. corethrurus*	1.2	0.64	1.35	1.51	11.85	14	12	−14.29
Mexico	La Mancha	Maize	*P. corethrurus*	0	0.64	0.84	1.48	76.19	7	7.7	10.00
Mexico	La Mancha	Maize	*P. corethrurus*	0.77	0.64	1.59	1.52	−4.40	8.4	8.4	0
Peru	Yurimaguas	Maize	*P. corethrurus*	0	0.28	1.09	1.53	40.37	1.89	2.52	33.33
Peru	Yurimaguas	Maize	*P. corethrurus*	0.25	0.28	1.22	1.70	39.34	2.55	2.65	3.92
Peru	Yurimaguas	Maize	*P. corethrurus*	0.43	0.28	1.62	2.13	31.48	2.05	3.12	52.20
Peru	Yurimaguas	Rice	*P. corethrurus*	0	0.28	0.77	1.57	103.90	1.28	2.13	66.41
Peru	Yurimaguas	Rice	*P. corethrurus*	0.25	0.28	0.78	1.62	107.69	2.09	1.8	−13.88
Peru	Yurimaguas	Rice	*P. corethrurus*	0.56	0.28	0.95	1.49	56.84	1.31	2.71	106.87
Peru	Yurimaguas	Cowpea	*P. corethrurus*	0	0.28	0.84	0.85	1.19	1.23	1.16	−5.69
Peru	Yurimaguas	Cowpea	*P. corethrurus*	0.21	0.28	0.91	0.78	−14.29	1.28	1.86	45.31
Peru	Yurimaguas	Cowpea	*P. corethrurus*	0.52	0.28	1.24	1.22	−1.61	1.52	1.69	11.18
Peru	Yurimaguas	Rice	*P. corethrurus*	0	0.28	0.73	1.12	53.42	1.56	2.71	73.72
Peru	Yurimaguas	Rice	*P. corethrurus*	0.12	0.28	1.02	1.53	50.00	2.35	2.6	10.64
Peru	Yurimaguas	Rice	*P. corethrurus*	0.32	0.28	1.39	2.00	43.88	2.32	3.14	35.34
Peru	Yurimaguas	Rice	*P. corethrurus*	0	0.28	0.86	0.71	−17.44	1.39	0.98	−29.50
Peru	Yurimaguas	Rice	*P. corethrurus*	0.27	0.28	1.16	0.66	−43.10	1.09	1.92	76.15
Peru	Yurimaguas	Rice	*P. corethrurus*	0.56	0.28	1.59	0.95	−40.25	1.88	1.23	−34.57
Peru	Yurimaguas	Rice	*P. corethrurus*	0	0.28	0.30	0.94	213.33	0.98	2.82	187.76
Peru	Yurimaguas	Rice	*P. corethrurus*	0.1	0.28	1.10	1.21	10.00	1.82	3.22	76.92
Peru	Yurimaguas	Rice	*P. corethrurus*	0.37	0.28	1.70	1.95	14.71	2.64	4.08	54.55
Peru	Yurimaguas	Maize	*P. corethrurus*	0.25	0.28	1.18	1.49	26.96	2.51	2.85	13.63
Peru	Yurimaguas	Maize	*P. corethrurus*	0.29	0.28	0.66	2.90	341.19	2.6	2.9	11.78
Peru	Yurimaguas	Maize	*P. corethrurus*	0.29	0.28	0.12	0.78	525.00	1.85	2.68	44.96
Peru	Yurimaguas	Maize	*P. corethrurus*	0.28	0.28	0.83	0.53	−36.42	1.6	2.14	33.54
Peru	Yurimaguas	Maize	*P. corethrurus*	0.21	0.28	1.86	2.89	54.99	5.23	7.13	36.32
Peru	Yurimaguas	Maize	*P. corethrurus*	0.71	0.28	1.36	2.44	79.21	2.02	2.48	22.56
Peru	Yurimaguas	Maize	*P. corethrurus*	0.25	0.28	0.00	0.09		4.81	3.66	−23.89
Peru	Yurimaguas	Maize	*P. corethrurus*	0.37	0.28	2.36	2.80	18.80	4.62	3.81	−17.51
Peru	Yurimaguas	Maize	*P. corethrurus*	0.38	0.28	2.37	1.94	−18.07	4.83	3.94	−18.48
Peru	Yurimaguas	Maize	*P. corethrurus*	0.39	0.28	1.43	0.93	−34.71	5.85	5.3	−9.48

Root yield (t ha^{-1})			Shoot/root			Total yield (t ha^{-1})			Earthworm mass (g m^{-2})			
Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Initial added	Final	% Survival[b]	Mass difference[c]
27.08	31.81	17.44	0.03	0.03	13.92	27.80	32.76	17.86	25	10.18	40.72	5.67
31.67	30.56	–3.51	0.01	0.02	28.69	32.13	31.13	–3.11	28.5	4.5	15.79	4.27
3.61	5.97	65.38	0.07	0.06	–21.27	3.88	6.32	62.97	30	2.58	8.60	2.70
									27	20.23	74.93	19.70
									27	21.58	79.93	21.50
									27	41.42	153.41	36.00
									27	10.05	37.22	5.00
									16	31.39	196.19	21.00
									16	25.93	162.06	21.00
									31.39	2.53	8.06	2.00
									25.93	2.04	7.87	–5.00
									27	15	55.56	–2.00
									27	9.21	34.11	–2.50
									16	3.24	20.25	0.80
									16	2.26	14.13	2.00
0.26	0.25	–5.26	13.91	13.76	–1.06	6.95	7.26	4.40	52.1	8.4	16.12	8.50
0.79	0.67	–15.59	24.08	28.53	18.47	21.89	22.35	2.09	35.5	8.12	22.87	7.86
0.77	0.73	–4.68	14.30	16.37	14.45	14.00	15.18	8.46	35.5	23.7	66.76	21.30
0.538	0.599	11.33	14.50	13.69	–5.58	8.34	8.80	5.53	35.5	11.5	32.39	7.71
0.704	0.727	3.27	13.49	12.65	–6.22	10.20	9.93	–2.71	35.5	19.6	55.21	9.98
0.151	0.243	60.9	13.91	9.05	–34.90	2.25	2.44	8.53	35.5	19.8	55.77	3.40
0.297	0.333	12.1	10.44	9.91	–5.06	3.40	3.63	6.95	35.5	28.1	79.15	–3.60
0.57	0.57	0.71	9.19	11.40	24.12	7.90	9.09	15.12	35.5	10.1	28.45	1.70
0.82	0.69	–15.37	6.95	10.09	45.10	8.52	9.74	14.37	35.5	17	47.89	–5.20
0.35	0.36	4.61	54.76	55.10	0.62	20.35	21.79	7.11	35.5	21.4	60.28	–3.20
0.53	0.50	–5.13	26.62	24.05	–9.65	15.88	14.01	–11.76	35.5	20.3	57.18	–21.60
0.37	0.40	8.31	18.77	19.06	1.56	8.21	9.58	16.69	35.5	38.2	107.61	9.60
0.41	0.45	11.82	20.69	18.50	–10.57	10.40	10.37	–0.21	35.5	31.9	89.86	–31.60
0.20	0.44	120.00	9.45	5.73	–39.39	3.18	4.49	41.19	36	27.5	76.39	27.50
0.40	0.33	–17.50	6.38	8.03	25.97	4.17	4.68	12.23	36	35.3	98.06	35.30
0.22	0.34	54.55	9.32	9.18	–1.52	3.89	5.59	43.70	36	32.5	90.28	32.50
0.29	0.54	86.21	4.41	3.94	–10.63	2.34	4.24	81.20	36	47.4	131.67	47.40
0.29	0.37	27.59	7.21	4.86	–32.50	3.16	3.79	19.94	36	42.1	116.94	42.10
0.16	0.47	193.75	8.19	5.77	–29.58	2.42	4.67	92.98	36	81.4	226.11	81.40
0.05	0.05	0.00	24.60	23.20	–5.69	2.12	2.06	–2.83	36	26	72.22	26.00
0.04	0.04	0.00	32.00	46.50	45.31	2.23	2.68	20.18	36	38.1	105.83	38.10
0.07	0.04	–42.86	21.71	42.25	94.57	2.83	2.95	4.24	36	80.5	223.61	80.50
0.28	0.50	78.57	5.57	5.42	–2.72	2.57	4.33	68.48	36	16.2	45.00	16.20
0.33	0.47	42.42	7.12	5.53	–22.32	3.70	4.60	24.32	36	24.3	67.50	24.30
0.37	0.53	43.24	6.27	5.92	–5.51	4.08	5.67	38.97	36	23.4	65.00	23.40
0.32	0.15	–53.13	4.34	6.53	50.41	2.57	1.84	–28.40	36	15.3	42.50	15.30
0.16	0.25	56.25	6.81	7.68	12.73	2.41	2.83	17.43	36	30.3	84.17	30.30
0.29	0.28	–3.45	6.48	4.39	–32.24	3.76	2.46	–34.57	36	45.8	127.22	45.80
0.22	0.54	145.45	4.45	5.22	17.23	1.50	4.30	186.67	36	48.3	134.17	48.30
0.45	0.77	71.11	4.04	4.18	3.40	3.37	5.20	54.30	36	54.3	150.83	54.30
0.39	0.89	128.21	6.77	4.58	–32.28	4.73	6.92	46.30	36	71.4	198.33	71.40
									36	35.3		
									0	42.1		
									0	38.1		
									0	24.3		
									0	30.3		
									0	54.3		
									0	35.3		
									0	42.1		
									0	38.1		
									36	24.3		

Continued

Appendix 4.1. *Continued.*

						Grain yield (t ha⁻¹)			Shoot yield (t ha⁻¹)		
Country	Location	Crop	Earthworm species	Residues (kg m^{-2})	Plot size (m^2)	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]
Peru	Yurimaguas	Maize	*P. corethrurus*	0.59	0.28	1.87	2.96	58.17	10.47	9.46	−9.6
Peru	Yurimaguas	Maize	*P. corethrurus*	0.95	0.28	0.62	0.63	1.46	6.37	5.57	−12.55
Peru	Yurimaguas	Maize	*P. corethrurus*	0	1250	1.29	0.36	−72.09			
Peru	Yurimaguas	Maize	*P. corethrurus*	0	1250	0.90	0.83	−7.78			
Peru	Yurimaguas	Cassava	*P. corethrurus*	0	1250						
Peru	Yurimaguas	Rice	*P. corethrurus*	0	1250	1.31	1.23	−6.11			
Peru	Yurimaguas	Cowpea	*P. corethrurus*	0	1250	0.51	0.37	−27.45			
Peru	Yurimaguas	Rice	*P. corethrurus*	0	1250	0.53	0.51	−4.16			
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.02	2.67	161.31
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.01	2.96	192.67
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.43	4.21	195.30
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				0.98	3.00	206.44
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				0.97	2.84	192.98
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				0.43	1.64	279.63
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				0.68	2.14	215.29
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				0.93	4.18	351.84
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.12	3.70	231.48
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.23	5.10	315.56
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.00	2.34	135.11
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.07	2.58	141.57
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.36	4.43	226.12
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.12	2.96	164.29
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.09	3.14	188.24
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				0.46	1.60	245.57
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				0.58	2.07	255.40
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.21	4.27	253.52
India	Sheikamuldi	Tea	*P. corethrurus et al.*	0	0.54				1.22	3.09	152.49
India	Sheikamuldi	Tea	*P. corethrurus et al.*	21.75	0.54				1.50	5.15	242.66
India	Sambalpur	Rice	*D. willsii*	0	4.65				15.57	16.8	8.03
India	Sambalpur	Rice	*D. willsii*	2.15	4.65				16.82	22.9	36.27
India	Sambalpur	Rice	*D. willsii*	0	4.65				19.9	20.8	4.37
India	Sambalpur	Rice	*D. willsii*	2.15	4.65				20.55	24.8	20.73
Australia	Narayen	Grasses	*Diplotrema* sp. nov. 1	0	0.5	1.08	1.49	39.00	3.16	5.75	81.91
Australia	Narayen	Grasses	*P. corethrurus*	0	0.5	1.40	1.50	6.59	3.16	4.46	40.99
Australia	Narayen	Grasses	*A. trapezoides + E. rosea*	0	0.5	1.37	1.57	14.33	3.16	4.67	47.75
Australia	Narayen	Grasses	*E. eugeniae*	0	0.5	1.48	1.81	22.87	3.16	5.81	83.87
Australia	Narayen	Grasses	*D. affinis + saliens*	0	0.5				3.16	4.55	43.90
Australia	Narayen	Grasses	*D. barwelli + A. minimus*	0	0.5				3.16	5.96	88.43
Australia	Samford	Grasses	*P. corethrurus*	0	0.5				5.99	8.89	48.25
Australia	Samford	Grasses	*A. trapezoides + E. rosea*	0	0.5				5.99	6.69	11.68
Australia	Samford	Grasses	*E. eugeniae*	0	0.5				5.99	6.44	7.41
Australia	Samford	Grasses	*D. affinis+saliens*	0	0.5				5.99	6.03	0.60
Australia	Samford	Grasses	*D. barwelli + A. minimus*	0	0.5				5.99	8.32	38.84
Australia	Samford	Grasses	*A. rodericensis*	0	0.5				5.99	9.26	54.45
Australia	Samford	Grasses	*P. taprobanae*	0	0.5				5.99	7.51	25.36
Brazil	Guarapuava	Beans	*Amynthas* sp.	0	1	1.01	1.07	5.93	2.05	1.81	−11.83
Brazil	Guarapuava	Beans	*Amynthas* sp.	0	1	1.01	1.02	0.89	2.05	2.12	3.27
Brazil	Guarapuava	Beans	*Amynthas* sp.	0	1	1.01	1.10	8.70	2.05	2.04	−0.23
Brazil	Guarapuava	Wheat	*Amynthas* sp.	0	1	1.44	1.48	2.78	3.63	4.02	10.94
Brazil	Guarapuava	Wheat	*Amynthas* sp.	0	1	1.44	1.49	3.61	3.63	3.85	6.19
Brazil	Guarapuava	Wheat	*Amynthas* sp.	0	1	1.44	1.58	9.38	3.63	4.25	17.28
Brazil	Curitiba	*Mimosa scabrella*	*Amynthas* sp.	2.23	2.70				4.87	6.97	43.21
Brazil	Curitiba	*M. scabrella*	*Amynthas* sp.	2.23	2.70				4.87	8.20	68.52
Brazil	Curitiba	*M. scabrella*	*Amynthas* sp.	2.23	2.70				4.87	7.26	49.25

Root yield (t ha⁻¹)			Shoot/root			Total yield (t ha⁻¹)			Earthworm mass (g m⁻²)			
Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Initial added	Final	% Survival[b]	Mass difference[c]
									36	30.3		
									36	54.3		
									1.31	1.88	143.51	3.75
									5.04	7.76	153.97	18.54
17.10	11.50	–32.75							0.96	5.53	576.04	1.90
									3.84	7.34	191.15	7.14
									7.34	10.13	138.01	11.08
									3.84	4.3	111.98	3.23
									14			
									14			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									0			
									648	18.82	2.90	–9.26
									648	106.64	16.46	98.97
									12.9	71.25	552.33	71.25
									12.9	116.25	901.16	116.25
									12.9	90	697.67	90.00
									12.9	101.25	784.88	101.25
									8.00	0	0	0
									164.00	0.07	0.04	0.07
									165.88	3.30	1.99	3.20
									140.00	0	0	0
									6.66	0	0	0
									24.00	0	0	0
									164.00	2.90	1.77	0.70
									165.88	0.55	0.33	–1.40
									140.00	0	0[??]	–1.63
									6.66	0	0[??]	–2.05
									24.00	0.15	0.63	–1.80
									28.28	0.15	0.53	–2.13
									136.00	27.57	20.27	25.33
									30.00			
									60			
									90.00			
									30.00	45.81	152.70	45.81
									60.00	61.33	102.22	61.33
									90.00	66.40	73.78	66.40
									30.00			
									60.00			
									90.00			

Continued

Appendix 4.1. *Continued.*

						Grain yield (t ha^{-1})			Shoot yield (t ha^{-1})		
Country	Location	Crop	Earthworm species	Residues (kg m^{-2})	Plot size (m^2)	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]
Ivory Coast	Lamto	Maize	*M. anomala*	0	0.04				0.16	0.65	309.52
Ivory Coast	Lamto	Maize	*M. anomala*	0	0.04				0.16	0.26	65.08
Ivory Coast	Lamto	Maize	*M. anomala*	0	0.04				0.16	0.59	273.02
Ivory Coast	Lamto	Maize	*P. corethrurus*	0	0.04				0.16	0.34	112.70
Ivory Coast	Lamto	Maize	*H. africanus*	0	0.04				0.16	0.20	28.57
Ivory Coast	Lamto	Maize	*S. porifera + C. zielae*	0	0.04				0.16	0.30	92.06
Ivory Coast	Lamto	*Panicum maximum*	*M. anomala*	0	0.04				0.94	1.70	81.78
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				0.94	2.36	151.76
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				0.94	2.35	150.37
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				0.94	3.25	247.07
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				0.94	2.72	190.26
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				6.66	10.08	51.41
Ivory Coast	Lamto	*P. maximum*	*M. anomala*	0	0.04				6.66	5.97	−10.29
Ivory Coast	Lamto	*P. maximum*	*S. porifera + C. zielae*	0	0.04				0.94	1.75	86.23
Ivory Coast	Lamto	*P. maximum*	*S. porifera + C. zielae*	0	0.04				0.94	2.94	214.03
Ivory Coast	Lamto	Rice	*S. porifera + C. zielae*	0	0.053	1.24	1.09	−11.99	1.55	1.66	7.10
Ivory Coast	Lamto	Rice	*H. africanus*	0	0.053	1.24	1.28	3.19	1.55	1.42	−8.39
Ivory Coast	Lamto	Rice	*M. anomala*	0	0.053	1.24	1.21	−2.43	1.55	1.59	2.58
Ivory Coast	Lamto	Rice	*M. anomala et al.*	0	0.053	1.24	1.51	21.70	1.55	1.76	13.55
Ivory Coast	Lamto	Peanuts	*S. porifera + C. zielae*	0	0.053	2.32	1.68	−27.72	2.92	3.04	4.11
Ivory Coast	Lamto	Peanuts	*H. africanus*	0	0.053	2.32	1.82	−21.71	2.92	2.87	−1.71
Ivory Coast	Lamto	Peanuts	*M. anomala*	0	0.053	2.32	1.73	−25.45	2.92	3.18	8.90
Ivory Coast	Lamto	Peanuts	*M. anomala et al.*	0	0.053	2.32	2.18	−6.26	2.92	3.02	3.42
Ivory Coast	Lamto	Maize	*S. porifera + C. zielae*	0	0.053	0.17	0.20	19.32	3.34	3.71	11.08
Ivory Coast	Lamto	Maize	*H. africanus*	0	0.053	0.17	0.26	54.55	3.34	3.65	9.28
Ivory Coast	Lamto	Maize	*M. anomala*	0	0.053	0.17	0.42	152.27	3.34	4.66	39.52
Ivory Coast	Lamto	Maize	*M. anomala et al.*	0	0.053	0.17	0.50	201.14	3.34	4.12	23.35
Mexico	La Vibora	Beans	*P. corethrurus*	0	0.009				0.17	0.19	8.28
Mexico	La Vibora	Beans	*P. elongata*	0	0.009				0.17	0.16	−8.92
Mexico	La Vibora	Beans	*P. corethrurus*	0	0.064				0.14	0.19	33.33
Mexico	La Vibora	Beans	*P. elongata*	0	0.064				0.14	0.34	144.44
Mexico	La Vibora	Beans	*P. corethrurus*	0	0.064	0.06	0.07	25.97	0.08	0.17	112.50
Mexico	La Vibora	Beans	*P. elongata*	0	0.064	0.06	0.06	1.66	0.08	0.2	150.00
Mexico	Los Tuxtlas	Maize	*P. corethrurus*	0	0.064	2.58	3.16	22.42	15.84	14.19	−10.42
Mexico	Los Tuxtlas	Maize	*P. corethrurus*	0.14	0.064	3.44	1.53	−55.51	13.55	10.58	−21.9
Mexico	Los Tuxtlas	Maize	*P. corethrurus*	0	0.009				0.94	0.81	−14.61
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				0.27	0.30	8.57
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				4.12	3.72	−9.68
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				0.24	0.20	−16.18
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				0.59	0.57	−4.40
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				2.91	2.73	−6.20
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.064				3.22	1.10	−65.80
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.049				0.67	0.81	21.21
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.049				0.47	0.63	34.78
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.049				6.49	5.02	−22.57
Mexico	La Vibora	*B. decumbens*	*P. corethrurus*	0	0.049				4.14	6.21	50.25
Peru	Yurimaguas	*Bixa orellana*	*P. corethrurus*	0	0.036				0.1486	1.87083	1158.879
Peru	Yurimaguas	*B. orellana*	*P. corethrurus*	0	0.036				0.15	1.64	1000.56
Peru	Yurimaguas	*B. orellana*	*P. corethrurus*	0	0.036				0.15	2.17	1357.01
Peru	Yurimaguas	*B. orellana*	*P. corethrurus*	0	0.036				0.80	1.64	106.78
Peru	Yurimaguas	*B. orellana*	*P. corethrurus*	0	0.036				0.80	2.23	180.48
Peru	Yurimaguas	*Bactris gasipaes*	*P. corethrurus*	0	0.036				0.80	0.46	−42.04
Peru	Yurimaguas	*B. gasipaes*	*P. corethrurus*	0	0.036				0.80	0.31	−60.74
Peru	Yurimaguas	*B. gasipaes*	*P. corethrurus*	0	0.036				0.80	0.41	−48.30

Root yield ($t\ ha^{-1}$)			Shoot/root			Total yield ($t\ ha^{-1}$)			Earthworm mass ($g\ m^{-2}$)			
Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Initial added	Final	% Survival[b]	Mass difference[c]
0.14	0.11	–21.43	1.13	5.86	421.21	0.30	0.76	153.78	25	30	120.00	30.00
0.14	0.07	–53.57	1.13	4.00	255.56	0.30	0.33	9.24	50	25	50.00	25.00
0.14	0.21	51.79	1.13	2.76	145.75	0.30	0.80	168.91	125	6.75	5.40	6.75
0.14	0.10	–28.57	1.13	3.35	197.78	0.30	0.44	46.22	50	0	0	0
0.14	0.06	–57.14	1.13	3.38	200.00	0.30	0.26	–11.76	50	0.25	0.50	0.25
0.14	0.18	28.57	1.13	1.68	49.38	0.30	0.48	62.18	25	22	88.00	22.00
1.62	2.67	64.79	0.58	0.64	10.31	2.56	4.38	71.01	25	72.5	290.00	72.50
1.62	3.88	139.13	0.58	0.61	5.28	2.56	6.24	143.75	50	107.5	215.00	107.50
1.62	3.52	117.08	0.58	0.67	15.34	2.56	5.87	129.27	75	85	113.33	85.00
1.62	4.45	173.92	0.58	0.73	26.70	2.56	7.70	200.69	100	127.5	127.50	127.50
1.62	4.19	158.01	0.58	0.65	12.50	2.56	6.91	169.81	127.5	95	74.51	95.00
3.91	7.57	93.35	1.70	1.33	–21.69	10.57	17.65	66.93	41	140	341.46	140.00
3.91	4.19	7.09	1.70	1.43	–16.23	10.57	10.16	–3.86	50	117.5	235.00	117.50
									12.5	36.25	290.00	36.25
									25	50.75	203.00	50.75
0.40	0.84	110.90	3.89	1.98	–49.22	3.19	3.59	12.61	56.5	36	63.72	32.60
0.40	0.31	–21.33	3.89	4.53	16.45	3.19	3.02	–5.49	56.5	6.4	11.33	3.00
0.40	0.63	58.77	3.89	2.52	–35.39	3.19	3.44	7.64	56.5	64.2	113.63	60.70
0.40	0.60	49.76	3.89	2.95	–24.18	3.19	3.87	21.24	56.5	76	134.51	72.60
0.92	1.08	18.35	3.19	2.81	–12.03	6.16	5.80	–5.77	56.5	19.6	34.69	19.6
0.92	0.68	–25.57	3.19	4.21	32.05	6.16	5.37	–12.80	56.5	13.8	24.42	13.8
0.92	0.89	–2.89	3.19	3.58	12.14	6.16	5.80	–5.80	56.5	52.6	93.10	52.6
0.92	0.81	–11.13	3.19	3.71	16.38	6.16	6.01	–2.39	56.5	32.3	57.17	32.3
1.53	1.44	–6.17	2.18	2.58	18.38	5.04	5.34	6.11	56.5	34	60.18	34
1.53	1.36	–11.34	2.18	2.69	23.26	5.04	5.26	4.51	56.5	12.3	21.77	12.3
1.53	1.51	–1.23	2.18	3.08	41.26	5.04	6.59	30.86	56.5	93.6	165.66	93.6
1.53	1.17	–23.43	2.18	3.52	61.09	5.04	5.79	15.00	56.5	43.2	76.46	43.2
0.08	0.07	–8.22	2.15	2.54	17.98	0.26	0.26	3.04	58.9	29.45	50.00	29.45
0.08	0.07	–13.70	2.15	2.27	5.54	0.26	0.23	–10.43	54.5	8.8	16.15	8.80
									61.8	107	173.14	107.00
									62.9	48.8	77.58	65.40
0.06	0.08	35.05	1.39	2.19	57.34	0.19	0.32	64.33	49.3	29.73	60.30	29.73
0.06	0.11	87.77	1.39	1.85	33.14	0.19	0.37	88.33	47.9	28.3	59.08	28.30
4.22	4.95	17.26	3.76	2.87	–23.60	22.64	22.29	–1.52	58.9	16.2	27.50	16.20
4.5	2.92	–35.01	6.0	5.3	–11.67	20.27	12.97	–36	60	37.36	62.26	37.36
0.52	0.41	–22.17	1.80	2.02	12.22	1.47	1.21	–17.3	32	0	0	0
									114.7	89.8	78.29	89.8
									113.9	71.4	62.69	71.4
0.04	0.04	0	5.61	4.7	–16.18	0.29	0.25	–14.04	117	91	78.27	91
0.16	0.19	20	18.16	14.19	–21.83	3.07	2.92	–4.82	116	73	62.9	73
0.05	0.07	39.22	11.59	7.96	–31.33	0.64	0.64	0.78	108	110	101.86	110
0.18	0.08	–58.47	17.61	14.15	–17.65	3.40	1.18	–65.34	117	89	75.52	89
0.13	0.13	–2.5	5.0	7.14	42.8	0.81	0.94	16.22	60.5	25.06	41.21	25.06
0.08	0.12	59.14	6.05	5.19	–14.12	0.54	0.75	38.36	61.93	25.06	41.4	25.06
0.39	0.73	88.31	11.58	9.53	–17.67	4.53	6.94	53.26	60.91	0	0	0
0.76	0.48	–37.05	10.15	10.91	7.41	7.25	5.50	–24.13	58.47	20.98	36.02	20.98
0.0361	0.588	1529.23	4.12	3.18	–22.73	0.18	2.46	1231.28	3.2	0	0.00	0.00
0.04	0.41	1033.08	4.12	4.00	–2.87	0.18	2.04	1006.92	10.6	14.7	138.68	14.70
0.04	0.63	1640.77	4.12	3.44	–16.30	0.18	2.79	1412.48	21.2	0	0.00	0.00
0.34	0.61	83.35	2.37	2.68	12.78	1.13	2.26	99.83	10.86			
0.34	1.05	214.58	2.37	2.11	–10.84	1.13	3.29	190.59	21.7			
0.45	0.31	–30.57	1.80	1.50	–16.53	1.24	0.77	–37.94	3.2	68	2125.00	68.00
0.45	0.24	–45.23	1.80	1.29	–28.32	1.24	0.56	–55.19	10.6	153	1443.40	153.00
0.45	0.29	–35.25	1.80	1.43	–20.15	1.24	0.70	–43.63	21.2	197.7	932.55	197.70

Continued

Appendix 4.1. *Continued.*

						Grain yield ($t\ ha^{-1}$)			Shoot yield ($t\ ha^{-1}$)		
Country	Location	Crop	Earthworm species	Residues ($kg\ m^{-2}$)	Plot size (m^2)	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]
Peru	Yurimaguas	*B. gasipaes*	*P. corethrurus*	0	0.036				1.69	1.86	10.10
Peru	Yurimaguas	*B. gasipaes*	*P. corethrurus*	0	0.036				1.69	1.70	0.71
Peru	Yurimaguas	*Eugenia stipitata*	*P. corethrurus*	0	0.036				0.24	0.57	138.15
Peru	Yurimaguas	*E. stipitata*	*P. corethrurus*	0	0.036				0.24	0.60	150.29
Peru	Yurimaguas	*E. stipitata*	*P. corethrurus*	0	0.036				0.24	0.86	258.15
Peru	Yurimaguas	*E. stipitata*	*P. corethrurus*	0	0.036				0.95	1.11	17.10
Peru	Yurimaguas	*E. stipitata*	*P. corethrurus*	0	0.036				0.95	1.17	23.37
India	Sambalpur	Rice	*D. willsii*	0	0.071	0.20	0.38	95.00			
India	Sambalpur	Rice	*D. willsii*	0	0.071	0.14	0.46	230.00	0.86	1.03	19.77
India	Sambalpur	Rice	*D. willsii*	0.28	0.071	0.20	0.59	200.00	0.89	1.37	53.93
India	Sambalpur	Tea	*P. corethrurus*	0	0.008				2.08	2.38	14.46
India	Sambalpur	Tea	*P. corethrurus*	25.5	0.008				2.38	2.68	12.63
India	Sambalpur	Tea	*P. corethrurus*	6.4	0.008				2.14	2.43	13.45
India	Sambalpur	Tea	*P. corethrurus*	31.8	0.008				2.68	3.08	14.95
India	Sambalpur	Tea	*P. corethrurus*	0	0.008				2.19	2.45	12.00
India	Sambalpur	Tea	*P. corethrurus*	25.5	0.008				2.43	3.80	56.70
India	Sambalpur	Tea	*P. corethrurus*	6.4	0.008				2.28	3.30	45.05
India	Sambalpur	Tea	*P. corethrurus*	31.8	0.008				3.69	4.83	30.85
Australia	Narayen	Grasses	*D. affinis*	0	0.043				3.99	5.77	44.61
Australia	Narayen	Grasses	*D. afinis*	0	0.043				8.58	11.16	30.04
Australia	Biloela	Sorghum	*P. elongata*	0	0.043	2.07	4.40	112.36	15.953	24.21	51.75
Australia	Biloela	Sorghum	*P. elongata*	0	0.043	2.67	2.95	10.43	17.302	17.4	0.56
Australia	Biloela	Sorghum	*O. occidentalis et al.*	0	0.043	2.67	3.05	13.91	17.302	15.3	−11.57
Australia	Biloela	Sorghum	*P. corethrurus*	0	0.043	2.67	4.05	51.30	17.302	19.72	13.97
Australia	Biloela	Sorghum	*A. trapezoides*	0	0.043	2.67	5.51	106.09	17.302	20.38	17.79
Australia	Narayen	Grasses	*D. affinis + saliens*	0	0.043				5.58	8.93	59.85
Australia	Narayen	Grasses	*S. minor*	0	0.043				5.58	4.01	−28.20
Australia	Narayen	Grasses	*P. corethrurus*	0	0.043				5.58	5.26	−5.79
Australia	Narayen	Grasses	*P. elongata*	0	0.043				5.58	3.74	−32.94
Australia	Narayen	Grasses	*P. taprobanae*	0	0.043				5.58	5.17	−7.37
Australia	Narayen	Grasses	*E. eugeniae*	0	0.043				5.58	6.58	17.83
Australia	Narayen	Grasses	*A. trapezoides*	0	0.043				5.58	7.42	32.90
Australia	Narayen	Grasses	*M. californica*	0	0.043				5.58	5.82	4.29
Australia	Narayen	Grasses	*F. unicus*	0	0.043				5.58	6.69	19.87
Australia	Narayen	Grasses	*E. saltensis*	0	0.043				5.58	5.15	−7.75
Australia	Narayen	Grasses	*D. bruneus*	0	0.043				5.58	4.43	−20.57
Australia	Kingaroy	Grasses	*D. affinis + saliens*	0	0.043				5.04	4.69	−6.96
Australia	Kingaroy	Grasses	*P. corethrurus*	0	0.043				5.04	5.48	8.72
Australia	Kingaroy	Grasses	*E. eugeniae*	0	0.043				5.04	4.68	−7.20
Australia	Kingaroy	Grasses	*A. trapezoides*	0	0.043				5.04	5.50	9.09
Australia	Kingaroy	Grasses	*F. unicus*	0	0.043				5.04	5.63	11.72
Australia	Samford	Grasses	*D. affinis + saliens*	0	0.043				3.61	6.20	71.60
Australia	Samford	Grasses	*P. corethrurus*	0	0.043				3.61	4.21	16.61
Australia	Samford	Grasses	*P. elongata*	0	0.043				3.61	4.76	31.68
Australia	Samford	Grasses	*P. taprobanae*	0	0.043				3.61	4.30	19.00
Australia	Samford	Grasses	*E. eugeniae*	0	0.043				3.61	3.91	8.37
Australia	Samford	Grasses	*A. trapezoides*	0	0.043				3.61	4.88	35.03
Australia	Samford	Grasses	*M. californica*	0	0.043				3.61	4.12	13.97
Australia	Samford	Grasses	*E. saltensis*	0	0.043				3.61	3.91	8.18
Australia	Narayen	Oats	*D. affinis + saliens*	0	0.043				9.07	10.43	14.92
Australia	Narayen	Oats	*S. minor*	0	0.043				9.07	7.54	−16.89
Australia	Narayen	Oats	*P. corethrurus*	0	0.043				9.07	10.00	10.20
Australia	Narayen	Oats	*P. elongata*	0	0.043				9.07	7.53	−16.94
Australia	Narayen	Oats	*P. taprobanae*	0	0.043				9.07	10.14	11.79
Australia	Narayen	Oats	*E. eugeniae*	0	0.043				9.07	11.69	28.89
Australia	Narayen	Oats	*A. trapezoides*	0	0.043				9.07	8.91	−1.82

Root yield (t ha^{-1})			Shoot/root			Total yield (t ha^{-1})			Earthworm mass (g m^{-2})			
Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Initial added	Final	% Survival[b]	Mass difference[c]
0.92	0.77	−15.89	1.84	2.41	30.91	2.60	2.63	0.95	10.86			
0.92	1.07	16.77	1.84	1.59	−13.76	2.60	2.77	6.36	21.7			
0.06	0.20	236.28	4.02	2.85	−29.18	0.30	0.77	157.69	3.2	217.5	6796.88	217.50
0.06	0.18	193.02	4.02	3.44	−14.58	0.30	0.78	158.80	10.6	199	1877.36	199.00
0.06	0.31	413.95	4.02	2.80	−30.31	0.30	1.17	289.17	21.2	205	966.98	205.00
0.43	0.46	7.55	2.20	2.40	8.88	1.38	1.57	14.11	10.86			
0.43	0.30	−29.48	2.20	3.85	74.96	1.38	1.47	6.85	21.7			
									42.4	56.6	133.49	56.60
0.65	0.69	6.52	1.33	1.49	12.43	1.65	2.18	32.52	42.4	63.7	150.24	63.70
0.77	1.20	54.55	1.15	1.14	−0.40	1.86	3.16	69.66	42.4	70.7	166.75	70.70
1.35	2.08	53.70	1.54	1.14	−25.53	3.43	4.45	29.93	127.3	264.8	208.01	264.80
1.20	2.16	80.21	1.98	1.24	−37.50	3.58	4.84	35.31	127.3	383.2	301.02	383.20
1.28	1.65	29.41	1.68	1.47	−12.33	3.41	4.08	19.41	127.3	300.5	236.06	300.50
1.61	1.58	−2.33	1.66	1.95	17.69	4.29	4.65	8.45	127.3	431.6	339.04	431.60
1.44	1.93	33.91	1.52	1.27	−16.36	3.63	4.38	20.69	127.3	99.3	78.00	99.30
1.51	3.88	156.20	1.60	0.98	−38.84	3.94	7.68	94.92	127.3	163	128.04	163.00
1.65	2.91	76.52	1.38	1.13	−17.82	3.93	6.21	58.28	127.3	220.3	173.06	220.30
2.25	2.16	−3.89	1.64	2.23	36.14	5.94	6.99	17.68	127.3	314.5	247.05	314.50
									23.06	92.22	399.99	92.22
									23.06	57.64	249.99	57.64
									325.96	274.60	84.24	274.60
									276.71	238.13	86.06	238.13
									23.45	14.07	60.00	14.07
									311.89	147.74	47.37	147.74
									262.64	35.18	13.39	35.18
13.07	10.79	−17.44	0.43	0.83	93.61	18.65	19.72	5.70	13.49	104.94	778.19	104.94
13.07	10.19	−22.06	0.43	0.39	−7.87	18.65	14.20	−23.90	45.34	10.32	22.76	10.32
13.07	9.93	−24.02	0.43	0.53	24.00	18.65	15.19	−18.56	49.41	111.04	224.74	111.04
13.07	7.60	−41.81	0.43	0.49	15.25	18.65	11.35	−39.16	82.54	320.68	388.52	320.68
13.07	13.44	2.85	0.43	0.38	−9.94	18.65	18.61	−0.21	112.76	170.48	151.19	170.48
13.07	9.93	−24.02	0.43	0.66	55.08	18.65	16.51	−11.49	99.98	67.42	67.44	67.42
13.07	10.42	−20.28	0.43	0.71	66.72	18.65	17.84	−4.36	70.91	80.26	113.18	80.26
13.07	10.07	−22.95	0.43	0.58	35.36	18.65	15.89	−14.80	127.88	73.87	57.77	73.87
13.07	12.30	−5.87	0.43	0.54	27.34	18.65	19.00	1.83	181.35	38.93	21.47	38.93
13.07	13.74	5.16	0.43	0.37	−12.27	18.65	18.90	1.30	13.95	23.45	168.10	23.45
13.07	15.02	14.95	0.43	0.30	−30.90	18.65	19.46	4.31	111.60	0.00	0.00	0.00
9.44	7.19	−23.89	0.53	0.65	22.24	14.48	11.88	−18.00	13.49	52.65	390.40	52.65
9.44	8.21	−13.05	0.53	0.67	25.04	14.48	13.69	−5.48	33.71	89.93	266.76	89.93
9.44	13.07	38.42	0.53	0.36	−32.96	14.48	17.75	22.54	99.98	28.73	28.73	28.73
9.44	8.33	−11.82	0.53	0.66	23.71	14.48	13.83	−4.54	51.15	69.88	136.62	69.88
9.44	11.12	17.73	0.53	0.51	−5.11	14.48	16.75	15.64	184.84	46.08	24.93	46.08
9.86	11.16	13.21	0.37	0.56	51.58	13.47	17.36	28.86	31.62	136.30	431.07	136.30
9.86	10.93	10.85	0.37	0.39	5.20	13.47	15.14	12.39	49.41	141.34	286.09	141.34
9.86	12.19	23.58	0.37	0.39	6.55	13.47	16.94	25.76	86.03	150.78	175.28	150.78
9.86	11.07	12.26	0.37	0.39	6.00	13.47	15.37	14.07	97.65	67.77	69.40	67.77
9.86	14.74	49.53	0.37	0.27	−27.52	13.47	18.66	38.49	101.14	104.24	103.06	104.24
9.86	11.51	16.75	0.37	0.42	15.66	13.47	16.39	21.65	55.22	61.03	110.52	61.03
9.86	9.81	−0.47	0.37	0.42	14.51	13.47	13.93	3.40	126.71	129.44	102.16	129.44
9.86	9.93	0.71	0.37	0.39	7.42	13.47	13.84	2.71	13.95	4.92	35.30	4.92
									13.49			
									45.34			
									49.41			
									82.54			
									112.76			
									99.98			
									70.91			

Continued

Appendix 4.1. *Continued.*

						Grain yield (t ha^{-1})			Shoot yield (t ha^{-1})		
Country	Location	Crop	Earthworm species	Residues (kg m^{-2})	Plot size (m^2)	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]
Australia	Narayen	Oats	*M. californica*	0	0.043				9.07	8.13	–10.38
Australia	Narayen	Oats	*F. unicus*	0	0.043				9.07	9.53	5.10
Australia	Narayen	Oats	*E. saltensis*	0	0.043				9.07	8.59	–5.33
Australia	Narayen	Oats	*Dig. bruneus*	0	0.043				9.07	8.72	–3.85
Australia	Kingaroy	Oats	*D. affinis + saliens*	0	0.043				7.63	6.54	–14.27
Australia	Kingaroy	Oats	*P. corethrurus*	0	0.043				7.63	7.27	–4.73
Australia	Kingaroy	Oats	*E. eugeniae*	0	0.043				7.63	6.17	–19.18
Australia	Kingaroy	Oats	*A. trapezoides*	0	0.043				7.63	5.81	–23.78
Australia	Kingaroy	Oats	*F. unicus*	0	0.043				7.63	6.10	–20.09
Australia	Samford	Oats	*D. affinis + saliens*	0	0.043				6.15	6.13	–0.34
Australia	Samford	Oats	*P. corethrurus*	0	0.043				6.15	5.63	–8.48
Australia	Samford	Oats	*P. elongata*	0	0.043				6.15	6.36	3.41
Australia	Samford	Oats	*P. taprobanae*	0	0.043				6.15	6.58	7.00
Australia	Samford	Oats	*E. eugeniae*	0	0.043				6.15	6.17	0.45
Australia	Samford	Oats	*A. trapezoides*	0	0.043				6.15	6.02	–2.08
Australia	Samford	Oats	*M. californica*	0	0.043				6.15	6.46	5.03
Australia	Samford	Oats	*E. saltensis*	0	0.043				6.15	5.87	–4.54
Australia	Narayen	Sorghum	*Diplotrema* sp. nov. 1	0	0.043				7.31	7.69	5.09
Australia	Narayen	Sorghum	*O. beatrix*	0	0.043				7.31	7.15	–2.23
Australia	Narayen	Sorghum	*E. rosea*	0	0.043				7.31	9.27	26.71
Australia	Narayen	Sorghum	*D. barwelli*	0	0.043				7.31	8.87	21.30
Australia	Narayen	Sorghum	*Diplotrema* sp. nov. 2	0	0.043				7.31	7.74	5.88
Australia	Narayen	Sorghum	*A. minimus*	0	0.043				7.31	7.38	0.95
Australia	Narayen	Sorghum	*H. bongeen*	0	0.043				7.31	10.21	39.59
Australia	Samford	Sorghum	*Diplotrema* sp. nov. 1	0	0.043				4.38	4.21	–3.98
Australia	Samford	Sorghum	*O. beatrix*	0	0.043				4.38	1.81	–58.62
Australia	Samford	Sorghum	*E. rosea*	0	0.043				4.38	4.37	–0.27
Australia	Samford	Sorghum	*D. barwelli*	0	0.043				4.38	4.12	–6.10
Australia	Samford	Sorghum	*A. minimus*	0	0.043				4.38	4.93	12.47
Australia	Samford	Oats	*P. excavatus*	0	0.043				2.51	2.48	–1.21
Australia	Samford	Oats	*E. eugeniae*	0	0.043				2.51	2.39	–4.55
Australia	Samford	Oats	*A. rodericensis*	0	0.043				2.51	2.38	–4.92
Australia	Narayen	Oats	*Diplotrema* sp. nov. 1	0	0.043				3.30	4.37	32.39
Australia	Narayen	Oats	*O. beatrix*	0	0.043				3.30	4.09	23.94
Australia	Narayen	Oats	*E. rosea*	0	0.043				3.30	5.23	58.45
Australia	Narayen	Oats	*D. barwelli*	0	0.043				3.30	4.49	35.92
Australia	Narayen	Oats	*Diplotrema* sp. nov. 2	0	0.043				3.30	3.35	1.41
Australia	Samford	Oats	*Diplotrema* sp. nov. 1	0	0.043				2.76	3.05	10.27
Australia	Samford	Oats	*O. beatrix*	0	0.043				2.76	3.40	22.90
Australia	Samford	Oats	*E. rosea*	0	0.043				2.76	2.91	5.22
Australia	Samford	Oats	*D. barwelli*	0	0.043				2.76	2.77	0.17
Cameroon	Mbalmayo	Maize	Unknown[d]	0	0.059				1.2441	2.1932	76.29
Cameroon	Mbalmayo	Maize	Unknown[d]	0.5	0.059				3.25	3.71	14.06
Martinique	St Anne	*D. decumbens*	*P. elongata*	0	50						
Martinique	St Anne	*D. decumbens*	*P. elongata*	0	50						
Martinique	St Anne	*D. decumbens*	*P. elongata*	0	50						
Martinique	St Anne	*D. decumbens*	*P. elongata*	0	50						

[a] % increase = (worm – control)/Control.

[b] % survival = 1 + [(Final earthworm mass – Initial earthworm mass)] / Initial earthworm mass.

[c] Mass difference = final earthworm mass in inoculated plot – mass in uninoculated plot.

[d] Several species (unidentified) were added.

[e] Not significantly different.

Root yield (t ha^{-1})			Shoot/root			Total yield (t ha^{-1})			Earthworm mass (g m^{-2})			
Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Control	Worm	% Increase[a]	Initial added	Final	% Survival[b]	Mass difference[c]
									127.88			
									181.35			
									13.95			
									111.60			
									13.49			
									33.71			
									99.98			
									51.15			
									184.84			
									31.62			
									49.41			
									86.03			
									97.65			
									101.14			
									55.22			
									126.71			
									13.95			
									29.08	56.51	194.35	56.51
									68.94	36.82	53.40	36.82
									137.89	0[??]	0[??]	0[??]
									39.87	66.60	167.06	66.60
									23.92	43.97	183.82	43.97
									44.79	33.42	74.61	33.42
									253.26	0	0	0
									27.44	0	0	0
									60.03	16.02	26.68	16.02
									134.84	3.13	2.32	3.13
									42.91	25.87	60.27	25.87
									40.57	9.22	22.74	9.22
									31.289	19.26	61.54	19.26
									96.28	13.24	13.75	13.24
									108.31	56.56	52.22	56.56
									29.08			
									68.94			
									137.89			
									39.87			
									23.92			
									27.44			
									60.03			
									134.84			
									42.91			
1.08	0.59	–45.44	1.15	3.73	223.12	2.32	2.78	19.78	164.1			
									164.1			
	n.s.d.[e]								90	35.7	39.7	35.6
	n.s.d.								90	46.6	51.8	46.4
	n.s.d.								90	32.8	36.4	32.2
	n.s.d.								90	42.3	47.0	39.2

Effects of Earthworms on Soil Structure and Physical Properties

5

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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

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(eds P. Lavelle, L. Brussaard and P. Hendrix)

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

Table 5.1. Characteristics of study sites.

	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* Eudrilid worms	*Pontoscolex corethrurus*	*Pontoscolex corethrurus*	*Pontoscolex corethrurus*	*Polypheretima elongata*	*Pontoscolex corethrurus*
Experimental crops	Maize (*Zea mays*) yam (*Diascorea alata*)	Maize (*Zea mays*) (six successive crops)	six successive crops: Maize, rice, cowpea, rice, rice, rice	*Brachiaria humidicola*	*Digitaria decumbens* Market-gardening crops	Tea gardens

Pot experiment	Maize, rice, peanut, *Panicum maximum*	Maize, beans				
Cast						
Production	x			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 *et al.* (1992)	Pashanasi *et al.* (1992), Alegre *et al.* (1995), Duboisset (1995)	Fontaine (1994)	Albrecht (1993) IRD-SECI (1994)	Senapati *et al.* (1994a) Senapati *et al.* (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 μm 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* casts than in non-ingested soil (Fig. 5.1). For swelling clayey soils such as

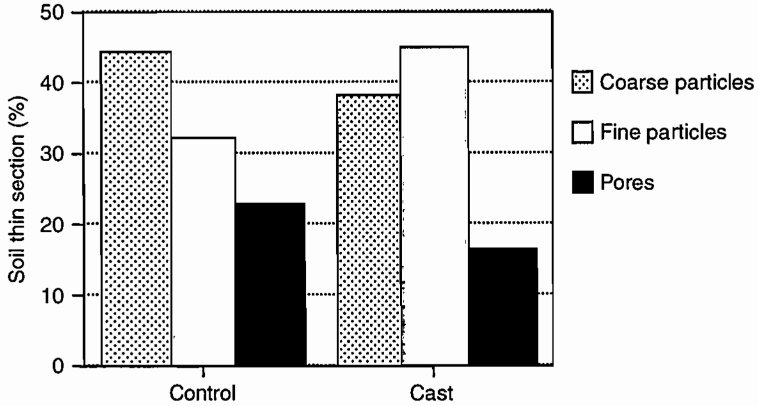

Fig. 5.1. Coarse and fine particles and pores in non-ingested soil (0–4 cm) and casts of *Pontoscolex corethrurus* (Yurimaguas, Peru), as a percentage of thin section surface (Duboisset, 1995).

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 $m^3\ Mg^{-1}$ (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 m^3 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 μm for soil, 27 μm for fresh casts and 210 μm for air-dried casts (Blanchart, unpublished data). At Lamto, large air-dried aggregates (> 10 mm) collected in treatments with earthworms

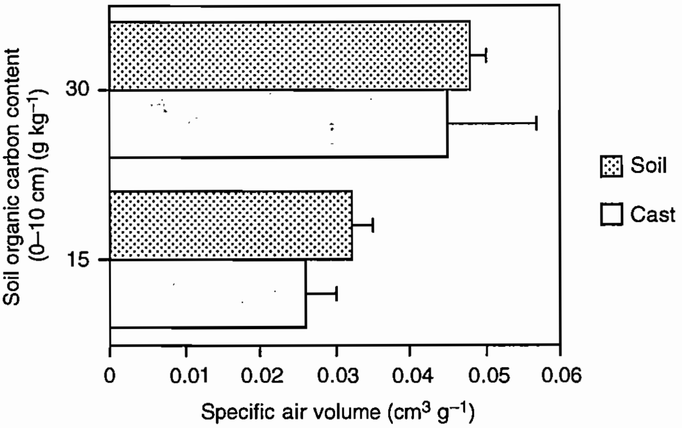

Fig. 5.2. Specific air volume of casts of *Polypheretima elongata* cultured in a low organic carbon (15 g C kg^{-1} soil) and a high organic carbon (30 g C kg^{-1} soil) Vertisol (Martinique) (mean and SE) (Blanchart, unpublished data).

(*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

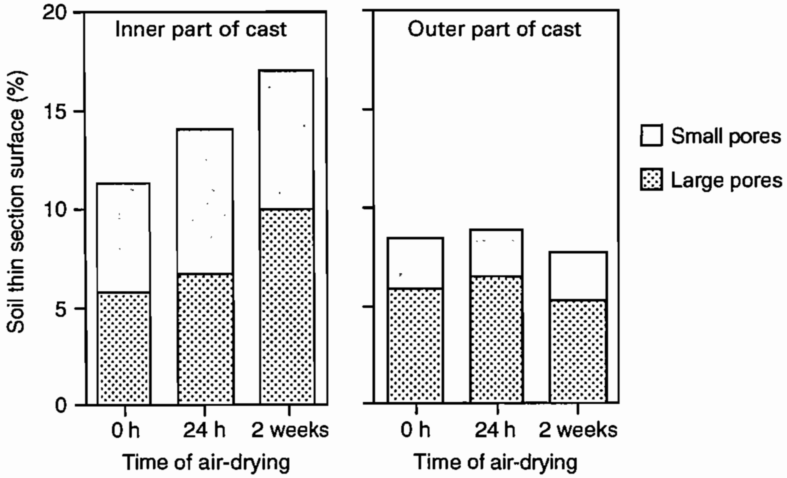

Fig. 5.3. Evolution with time of porosity (large and small pores) in the outer and inner parts of casts of *Pontoscolex corethrurus*, during air-drying (Yurimaguas, Peru) (Duboisset, 1995).

approximately 25 μm 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 μm) (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),

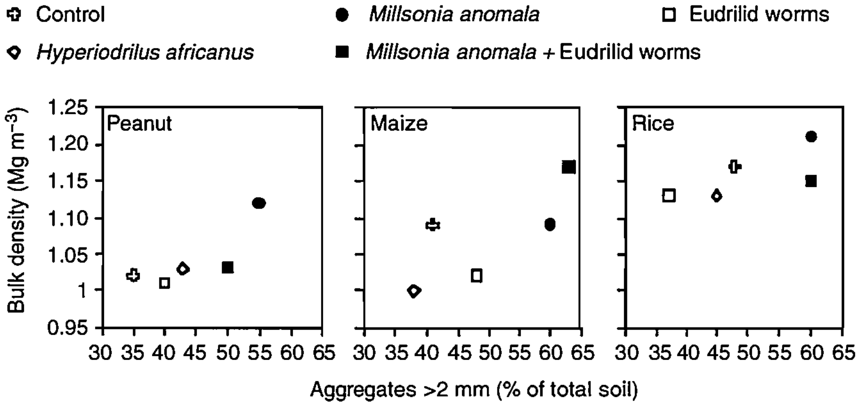

Fig. 5.4. Aggregation and bulk density in pot experiments at Lamto (Ivory Coast) for different earthworm populations and three crops (adapted from Derouard *et al.*, 1997).

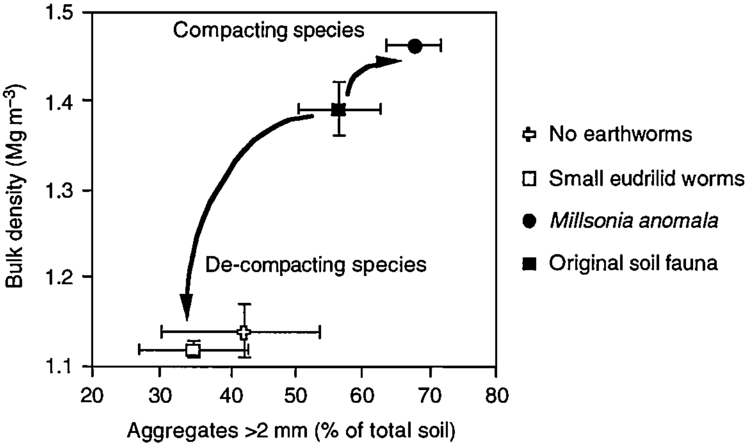

Fig. 5.5. Evolution of bulk density and macro-aggregates in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast) (adapted from Blanchart *et al.*, 1997).

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 (~1 mm) and microporosity (~10 μm) and a decrease of mesoporosity (~100 μm). As a consequence, bulk density increased, structural porosity tended to be equal to or lower than textural porosity, 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 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,

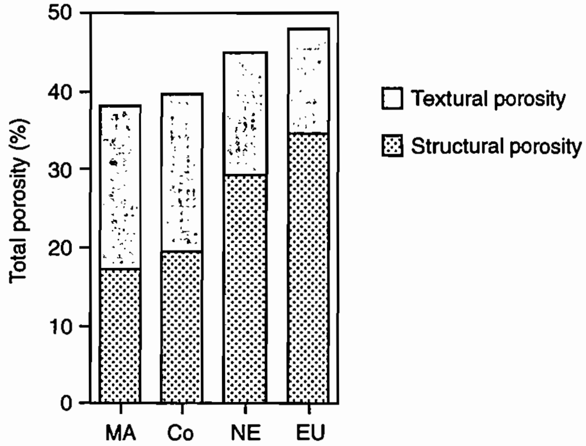

Fig. 5.6. Evolution of porosity (structural and textural) in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast). MA = *Millsonia anomala*, Co = control, NE = no earthworms, EU = eudrilid earthworms (adapted from Blanchart *et al.*, 1997).

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

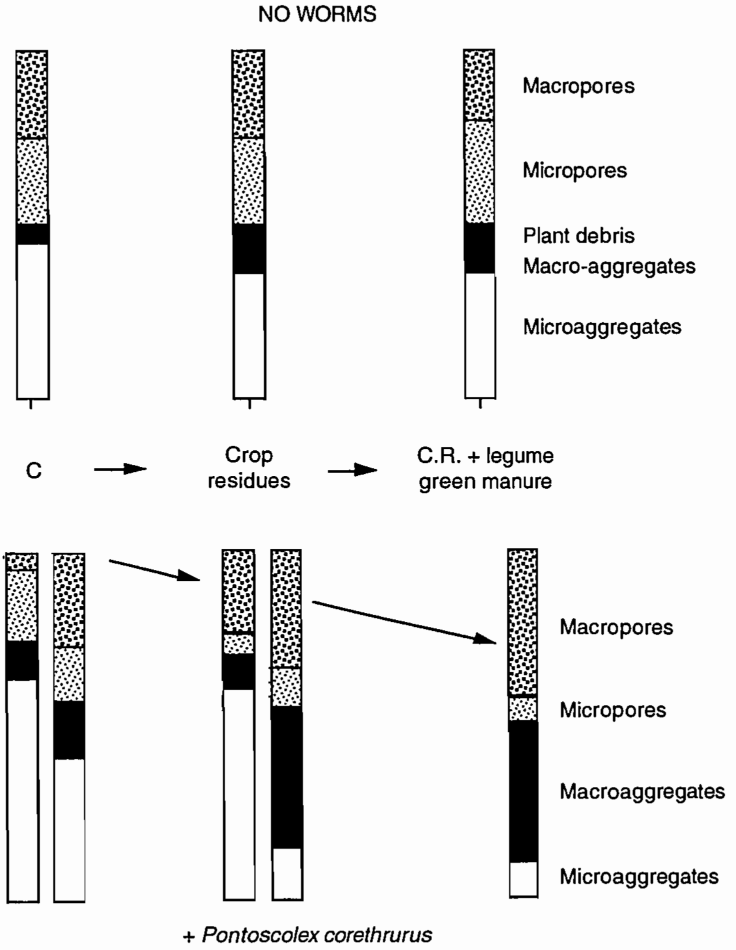

Fig. 5.7. Effects of earthworm introduction and crop residue application on aggregation (macro- and micro-aggregates), porosity (macro- and microporosity) and plant debris in the soil (0–4 cm) of Yurimaguas (Peru) as proportions of surface of soil thin sections. A = surface strata (0–1.5 cm), B = deeper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

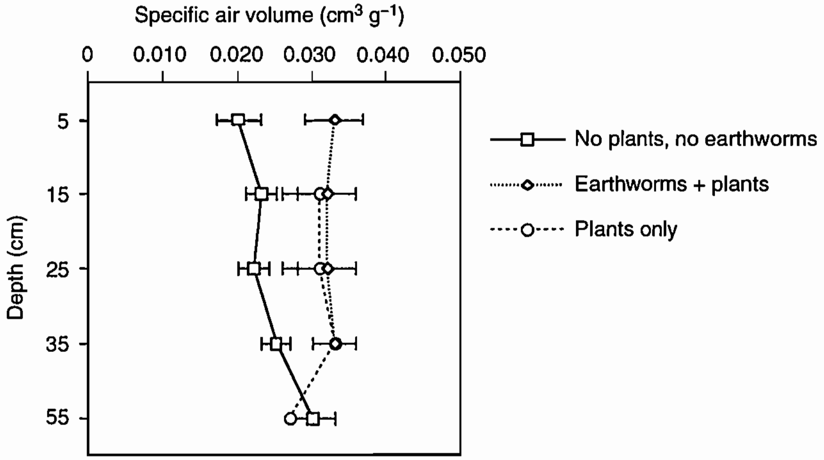

Fig. 5.8. Evolution with depth of specific air volume of 5 cm^3 aggregates in a Vertisol for three different treatments, after 1 year of experimentation (Martinique) (means and confidence interval $P < 0.05$, $n = 12$) (Blanchart, unpublished data 1994).

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 irrespective of the earthworm effect. In their experiment, modification of 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.

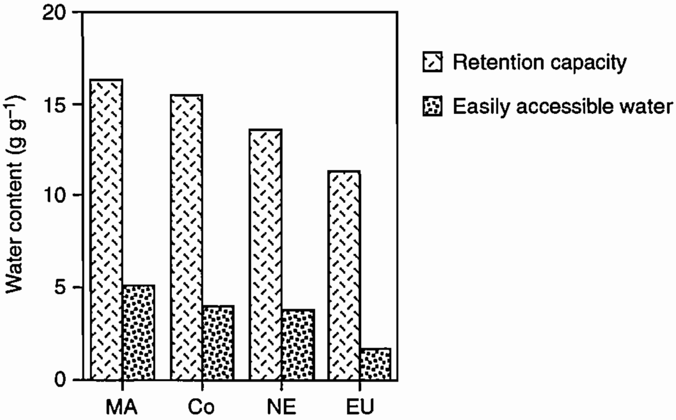

Fig. 5.9. Evolution of water retention capacity and easily accessible water in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast). MA = *Millsonia anomala*, Co = control, NE = no earthworms, EU = eudrilid earthworms (adapted from Blanchart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

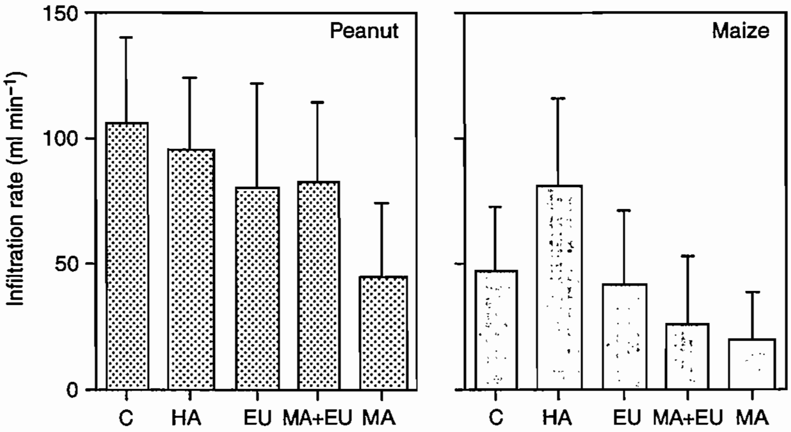

Fig. 5.10. Infiltration rate in a 2 mm sieved soil (pot experiments) with different earthworm populations and two crops after 80 days of experimentation.
C = control, HA = *Hyperiodrilus africanus*, EU = eudrilid earthworms,
MA = *Millsonia anomala*, EU + MA = association of eudrilid earthworms and *Millsonia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

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

6

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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

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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 μm) particles and an accumulation of small (< 2 μm) 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 m^2 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 ×.

	Mexico	Peru		Martinique (West Indies)	Ivory Coast	
	Continuous maize (*Zea mays*)	Crop rotation maize + rice + cowpea + rice (3)	Continuous maize (*Zea mays*)	Pasture (*Digitaria decumbens*)	Continuous yam (*Diascorea alata*)	Continuous maize (*Zea mays*)
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	*P. corethrurus*	*P. corethrurus*	*P. corethrurus*	*P. elongata*	*M. anomala*	*M. anomala*
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 *et al.* (unpublished data)	Pashanasi *et al.* (1996)	Charpentier (1996)	Blanchart *et al.* (unpublished data)	Gilot (1997)	Gilot (1994)

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[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 ^{13}C 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

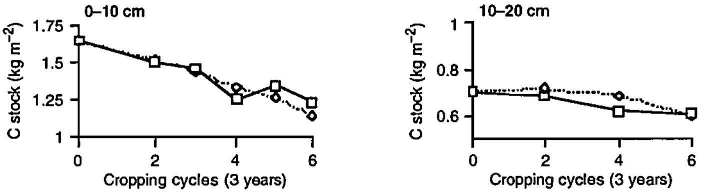
Changes of carbon stocks during the cultivation period

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.

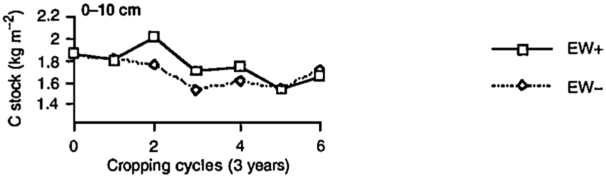
After 3 years of maize cultivation (six cropping cycles) at Lamto, the stock of C in the upper 10 cm of soil had decreased significantly from 1.64 kg m^{-2} to 1.14 and 1.23 kg m^{-2} in the control and inoculated treatments, respectively (Fig. 6.1a). The soil C lost after 3 years of cropping represented, 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.

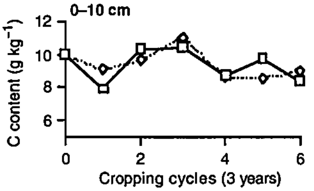
(a) C stock in the maize plot of Lamto in the 0–10 and 10–20 cm strata



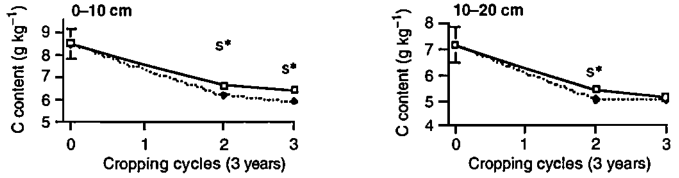
(b) C stock in the crop rotation at Yurimaguas in the upper 10 cm



(c) C content in the maize plot at La Mancha, in the upper 10 cm



(d) C content in the yam plot at Lamto, in the 0–10 and 10–20 cm strata



(e) C content in the digitaria plot of St Anne, in the 0–20 and 20–40 cm strata

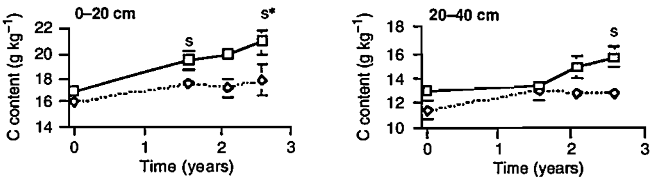


Fig. 6.1. Changes in the soil organic carbon (stocks or contents) in the different plots during 3 years of the experiment. Inoculated treatments are compared with control: significant differences are indicated on the graphs (bars = standard errors; s*, significant differences between treatments, $P < 0.10$; 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 $^{13}C/^{12}C$ ratio induced by vegetation changes from C_3 to C_4 photosynthetic pathways, particularly maize cultivation (C_4) after forest (C_3) clearing (Balesdent *et al.*, 1987; Mariotti, 1991). This natural labelling of SOM by the $^{13}C/^{12}C$ 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

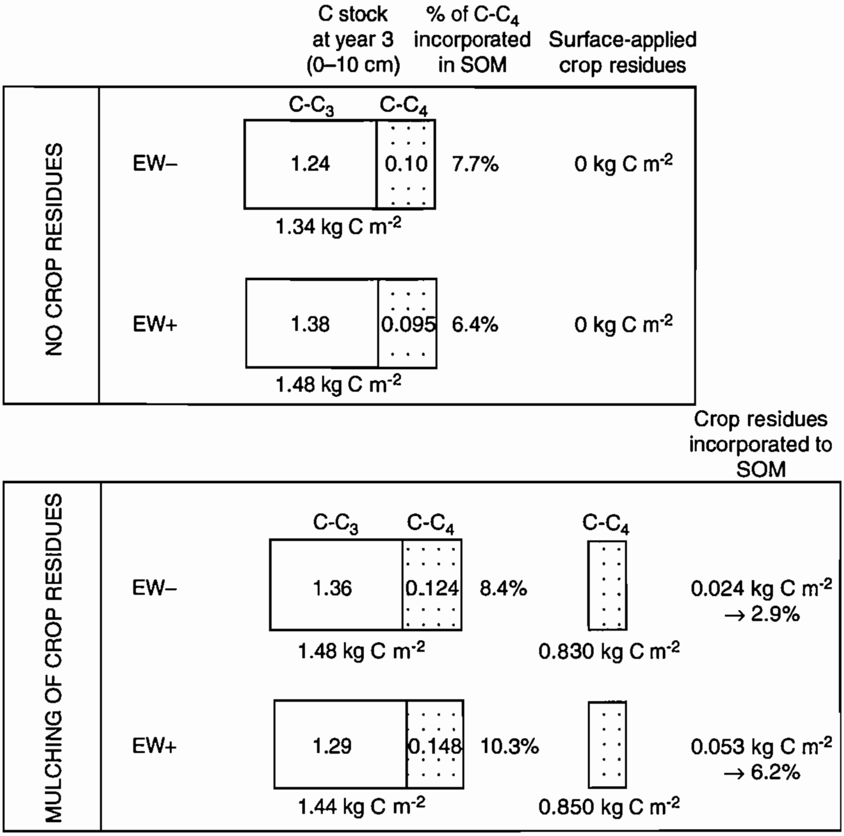


Fig. 6.2. Soil carbon budget (0–10 cm) in the continuous maize plot at Lamto after 3 years of cultivation (EW–: without earthworms, EW+: with earthworm inoculation). C-C3: C of the original forest soil; C-C4: C of fresh maize input. (Adapted from Gilot *et al*, 1995.)

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–C_4 incorporated into the SOM between EW-M+[1] and EW-M– represented 20% of the C-C_4 incorporated into EW-M+, while the increase of 53 g C m^{-2} between EW+M– and EW+M+ represented 36% of the C-C_4 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

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[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-C_4 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–C_4 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, C_4-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-C_4 m^{-2} from the maize was incorporated into the SOM in the upper 30 cm, representing 6.2% of total soil C. Total C-C_4 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).

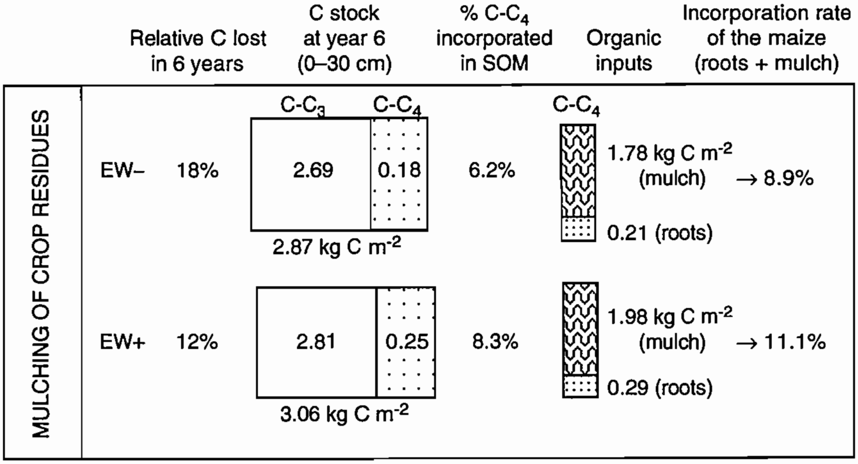


Fig. 6.3. Soil carbon budget (0–30 cm) in the continuous maize plot at Yurimaguas after 6 years of cultivation (EW–: without earthworms, EW+: with earthworm inoculation). C-C_3: C of the original forest soil, C-C_4: C of fresh maize input. (Adapted from Charpentier, 1996.)

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 μm), the organo-silt complex (2–20 μm) and the organo-clay compartment (< 2 μm). 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.

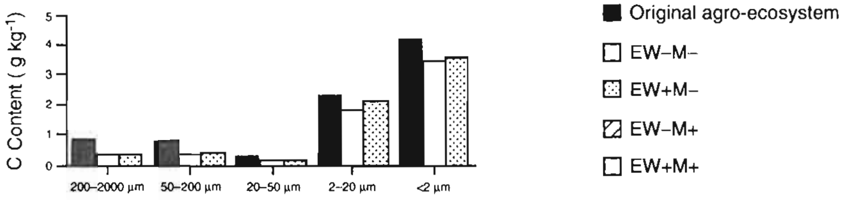
In the yam plot at Lamto, the slightly higher amount of C in inoculated treatments did not appear to be closely linked to a specific fraction of SOM (Gilot, 1997). However, the C remaining in the 2–20 μm fraction at the end of the experiment tended to be higher in the inoculated treatment than in the control (Fig. 6.4a). Before cropping, the savanna soil at Lamto had a high proportion (> 75%) of C contained in the finer fractions (< 20 μm); 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 μm.

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 (50–200 μm and 200–2000 μm), 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).

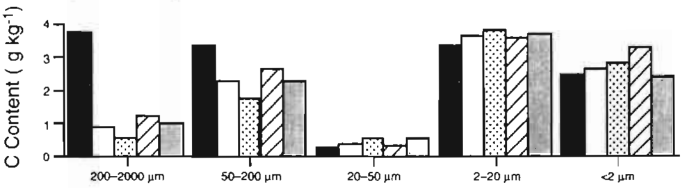
After 6 years of continuous maize cultivation at Yurimaguas, reduction of the C stock following land clearing was due to a decrease of the C contained in all fractions > 20 μm. As in the maize plot after forest clearing at Lamto, earthworm activity induced a decrease of the C contained in the coarse fractions (> 50 μm) (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

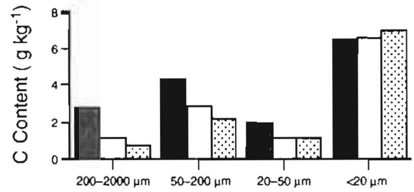
(a) Lamto, yam (3 years after earthworm introduction)



(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)

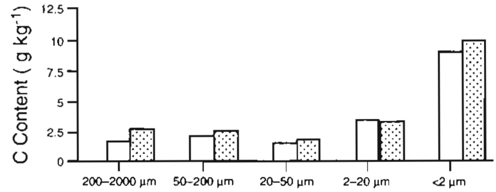


Fig. 6.4. Distribution of the total C of the soil among particle size fractions: comparison of the initial and final dates in the four plots (EW–: without earthworms, EW+: with earthworm inoculation; M–: exportation of the crop residues, M+: crop residues left on the soil surface). (Adapted from Gilot *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 μm) and in the finer ones (< 2 μm).

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.

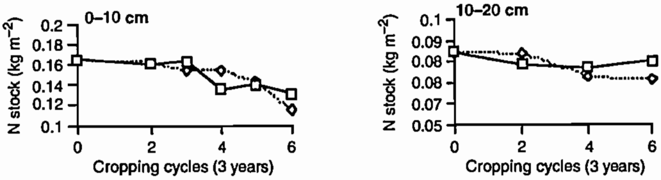
At La Mancha, nitrogen content decreased by 40% in the 0–10 cm depth during 3 years and was less variable than carbon content between dates; however, no difference between treatments was observed (Fig. 6.5c).

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).

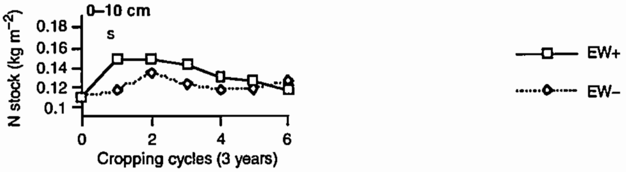
Following pasture establishment at St Anne, the nitrogen content increased significantly during 30 months in the non-inoculated control. A slight, but non-significant difference existed between the nitrogen content in the two treatments at the beginning of the experiment (Fig. 6.5e). Thirty months after 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.

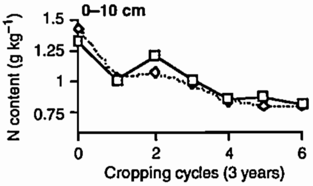
(a) N stock in the maize plot of Lamto in the 0–10 and 10–20 cm strata



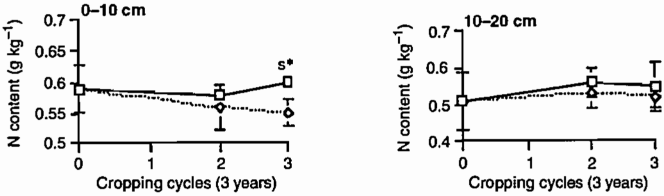
(b) N stock in the crop rotation at Yurimaguas in the first 10 cm



(c) N content in the maize plot at La Mancha, in the first 10 cm



(d) N content in the yam plot at Lamto, in the 0–10 and 10–20 cm strata



(e) N content in the digitaria plot of St Anne, in the 0–20 and 20–40 cm strata

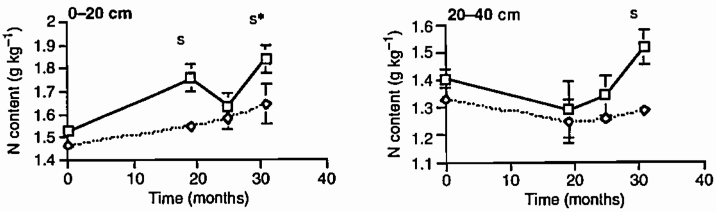


Fig. 6.5. Changes in the soil organic nitrogen (stocks or contents) in the different plots during 2 or 3 years of experimentation. Inoculated treatments are compared with control: significant differences are indicated on the graphs (bars = standard errors; s*, significant differences between treatments,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

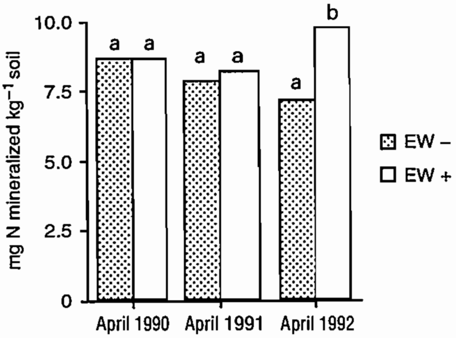


Fig. 6.6. Soil N mineralization in incubation experiments under laboratory conditions from a yam plot (Lamto 0–10 cm) in mg of total mineral nitrogen/100 g soil [before cultivation (1990); before the second (1991) and the third cropping period (1992)]. Significant differences are indicated on the graph (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.

			Final date (3 years of cropping)	
		Initial date	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

[a] Yurimaguas: six replicates per treatment; [b] Lamto: 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).

	Lamto		Yurimaguas		La Mancha	St Anne
Earthworm effect on	Yam	Maize	Rotation[a]	Maize	Maize	Pasture
	(0–10 cm)	(0–10 cm)	(0–10 cm)		(0–10 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; +/0, 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

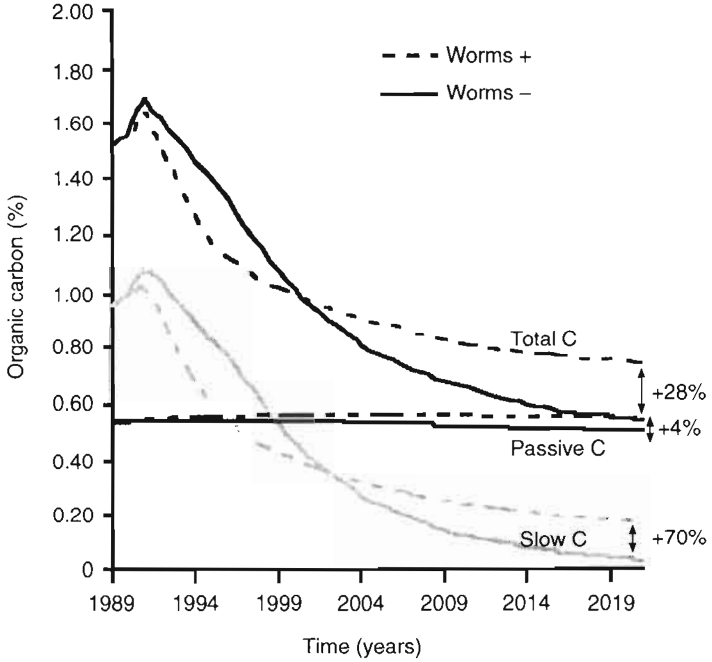


Fig. 6.7. Simulation of soil organic carbon dynamics using CENTURY after deforestation and 30 years of continuous cropping at Yurimaguas. (Adapted from Lierman, 1996.)

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-Villenave *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 μm and especially > 200 μm). 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 μm 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 μm) seems to be ingested preferentially by earthworms and partly comminuted, the non-digested part being accumulated in fractions of finer (< 20 μm) 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 digestability 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

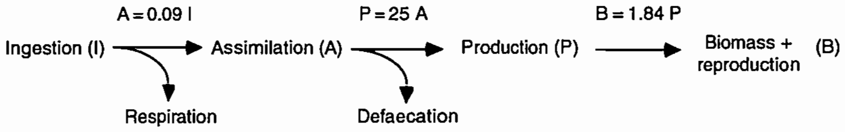


Fig. 6.8. Energy budget of an earthworm population [calculated for *Millsonia anomala* at Lamto (Ivory Coast). Lavelle, 1978].

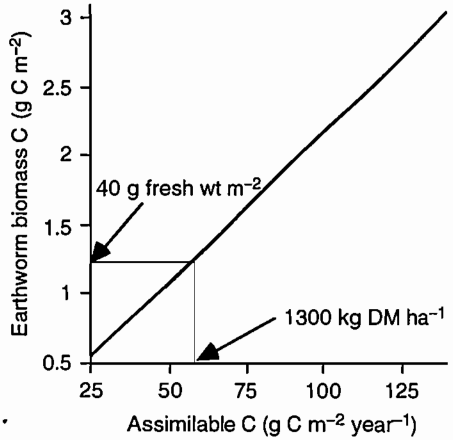


Fig. 6.9. Relationship between the biomass of an earthworm population of *Millsonia anomala* and the assimilable carbon needed for its nutrition.

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-Villenave *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.

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In-soil Earthworm Technologies for Tropical Agroecosystems

7

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Summary

Collaborative research in the Macrofauna project has enabled development of some techniques that presently are at different stages of advancement, from promising pilot experiments (tomato production and inoculation in plant nursery bags at Yurimaguas and in India) to the fully developed technique of massive worm production and biofertilization of tea gardens in Tamil Nadu (India) (patent deposited). Failures have also helped to gain better insight into the potential and feasibility of techniques that had been considered in the objectives of this project.

Endogeic earthworms (*Pontoscolex corethrurus*) may be produced in large quantities, i.e. about 12,000 worms (1.6–2.8 kg live wt) m^{-2} $year^{-1}$ in specific culture beds using either sawdust (Yurimaguas, Peru) or a mixture of high and low quality materials (Tamil Nadu, India) mixed into the soil as substrates. Cost of production of 1 kg of earthworm biomass through bed culture is about

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(eds P. Lavelle, L. Brussaard and P. Hendrix)

3.6 Euro, much lower than the cost of hand collection of worms from pastures/grasslands where these species are abundant (6–125 Euro depending on the cost of labour and earthworm density).

The theoretical value of an active earthworm community with an average biomass of 400 kg live wt has been estimated at 1400 Euro, the price that it would cost to reintroduce an equivalent biomass produced in our culture units, indicating the cost of land restoration.

Direct inoculation of earthworms in the field to improve production may only affect plant growth positively if a large biomass (> 30 g live wt m^{-2}) is inoculated from the beginning. An alternative may be to concentrate the inoculum in small areas regularly distributed across the field.

Due to the high price of earthworm production and inoculation, technologies that involve inoculation should only be applied to high value crops; examples tested in our project are: (i) tree seedling nurseries in Peru and India; (ii) tomato production in Peru; and (iii) tea gardens in India.

In most systems, techniques that maintain locally available earthworm communities should be considered. Experiments at Carimagua (Colombia) showed that: (i) the juxtaposition of plots under different crops with contrasting effects on earthworms did not seem to allow colonization of unfavourable sites from the favourable ones; (ii) some native species may survive, especially if tillage is done early in the rainy seasons when populations are in diapause deep in the soil out of reach of the plough; (iii) reconstitution of populations in a plot that has been replanted to a crop that is favourable to earthworms (e.g. an improved pasture at Carimagua) may be significant after a few years (2–4).

Recolonization patterns have been studied particularly at the SECI station of St Anne (Martinique) in a pasture planted on a degraded Vertisol. Recolonization originated from a few individuals that managed to adapt to conditions of the degraded soil by a combination of genetic selection, concentration in better suitable micro-environments and better growth and reproduction efficiencies. Massive reintroduction of earthworms significantly accelerated the establishment of populations, which otherwise were rather slow to develop in this system. There was no evidence that earthworm activities would accelerate the reconstitution of organic stocks. The only visible effect after 3 years was a difference in the vertical distribution of soil organic matter (SOM) with depth in the presence of earthworms.

Of the three techniques that have been developed successfully, two are promising, although further research is still needed before they can be widely used. They are: (i) inoculation of worms in nursery pots enhanced the growth of three out of the four species that were tested, and mycorrhizal infections were improved. Further experiments are needed to test for further survival and growth of these trees when planted in the field; (ii) tomatoes and other market gardening products were produced at Yurimaguas, Peru on a mixture of soil and sawdust. Supplementation of this substrate with essential nutrients (phosphorus and, to a lesser extent, nitrogen contained in chicken manure slurry) and improved disease control should increase production to satisfactory levels.

A great advantage of this technique is that it makes use of sawdust, a by-product of the timber industry that accumulates in suburban areas and may create environmental problems.

A third technique has been developed fully in India, in association with Parry Agro Industries Ltd, to stimulate growth of tea plants and enhance soil quality. This technique uses a combination of mechanical intervention (digging trenches in contour lines), input of organic matter of different qualities in a specific spatiotemporal design and the inoculation of earthworms produced locally using a special technology. Enhancement of production was 79.5–276%, and profit was increased in similar proportions, while soil quality was restored by large organic inputs and earthworm activities. This technique and the associated system for massive production of earthworms has been protected by a patent 'Fertilisation Bio-organique dans les Plantations Arborées' deposited in Sri Lanka (4/9/96 at Colombo, Ref. No. 11034) and internationally (ref. PCT/FR 97/01363). This technique has been extended currently to about 200 ha located at different sites of Parry Agro's plantations.

Introduction

Earthworms are a resource that may be used in agriculture because their effects on nutrient dynamics and the physical structure of soil may significantly enhance plant growth and conserve soil quality [see Chapters 1–6), reviewed by Lee (1985), and, more recently, by Lavelle *et al.* (1998)]. It has, therefore, been hypothesized that management options that stimulate the activities of these organisms could promote sustainable production in tropical agroecosystems (Swift, 1987; Myers *et al.*, 1994). Results from previous chapters suggest that the success of techniques of earthworm management may depend upon the choice of suitable species, the provision of adequate organic supplies to feed the worms and the maintenance of a minimum diversity in whole invertebrate communities. All these biological resources, therefore, need to be managed at the same time.

In the humid tropics, 'in-soil' technologies that incorporate organic residues into the soil to stimulate the activities of local or inoculated populations of soil-dwelling earthworms should be preferred in most cases to 'off-soil' techniques (vermicomposting) that simply use earthworms to prepare compost (Fig. 7.1). Vermicomposting of residues allows the quick transformation of fresh residues into a compost that can be used readily in the field (see Chapter 9). However, a large amount of C is lost that might have been used to sustain mechanical activities of earthworms and other invertebrates in the soil. Endogeic earthworms indeed participate in the humification of organic matter, but they also contribute to macro-aggregation of soil particles, maintenance of macroporosity and the intimate mixing of organic compounds, with expected effects on long-term sustainability of soil fertility (Blanchart *et al.*,

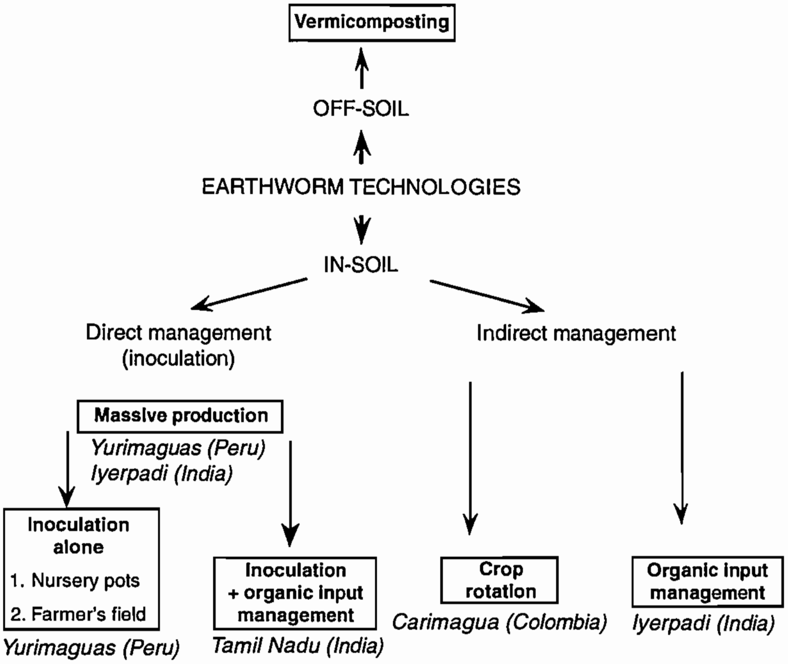

Fig. 7.1. Management alternatives for earthworm technology.

1997). Vermicomposting should only be recommended when either the quality, the amount or the location of organic residues make them unsuitable for local use in agriculture. In such conditions, vermicomposting generally produces a better compost with higher C and N contents and lower concentrations of aromatic C than a compost produced without worms (Vinceslas, 1998; Aranda *et al.*, Chapter 9).

In-soil technologies are based on the use of endogeic and anecic earthworms that significantly influence soil physical properties (see Chapter 5) and regulate the dynamics of soil organic matter on different scales of time and space (Chapter 6). These technologies manipulate earthworm communities, either directly through the massive inoculation of suitable populations, or indirectly by promoting suitable conditions for the activity of already existing populations through the manipulation of plant communities and/or organic inputs. Optimal levels of biomass to enhance soil fertility and crop yield significantly must be established through these technologies.

Different techniques have been developed in this project. They include the intensive production of the endogeic earthworm *Pontoscolex corethrurus* on different substrates to allow large-scale inoculations, enhancement of growth of tree seedlings in nursery pots and a new market gardening technique based on the joint use of earthworms and sawdust at Yurimaguas, Peru. Intensive production of endogeic and anecic earthworms in vermiculture units, growth stimulation of tea seedlings in nursery bags and biofertilization of tea plantations using diverse organic materials have been developed in Tamil Nadu (India). Indirect management techniques have been also investigated at St Anne (Martinique) and Carimagua (Colombia).

Earthworm Collection

In-soil technologies require mostly endogeic, endo-anecic to anecic earthworms with specific ecological characteristics (Chapter 3). These types of earthworms are not available commercially. Therefore, they can be collected from the field, which is labour intensive and may damage the natural system, or produced in intensive cultures made close to the inoculated fields or experimental units.

Costs of earthworm collection from natural environments has been calculated at St Anne (Martinique, French West Indies), Yurimaguas (Amazonia, Peru) and Pandalur (Tamil Nadu, India) (Table 7.1). Due to the high costs of labour at St Anne, the price for collecting 1 kg of fresh mass of the endogeic earthworm *Polypheretima elongata* was 125 Euro. This actually is a prohibitive price considering that a minimum inoculation of 300–400 kg of fresh biomass is necessary to produce significant effects on plant growth (Brown *et al.*, Chapter 4); intensive cultures are to be preferred.

Table 7.1. Cost of earthworm collection from natural environments at three sites.

	St Anne (Martinique)	Yurimaguas (Peru)	Pandalur (India)
Time to collect 1 kg of earthworms from the field (in days)*	2.25	4.2	4.5
Average weight (g live wt worm^{-1})	1.5**	0.5***	0.45***
Age classes	Mixed	Adults	Adults + late immatures
Cost of daily wage labourer (in Euro)	56	4.3	1.4
Cost of 1 kg of live earthworms (in Euro)	125	18	6.2

*Eight hours work, day^{-1}; ***Polypheretima elongata;* *** *Pontoscolex corethrurus.*

Earthworm Culture

The proportion of soil used in endogeic and anecic earthworm cultures is more than 50% of the substrate (Senapati, 1994). The most commonly used earthworms so far have been the endogeics *P. corethrurus* and *P. elongata*. Details regarding the biology and ecological strategies of these worms are given in Fragoso *et al.* (Chapters 1 and 2) and Barois *et al.* (Chapter 3). Small- and large-scale earthworm culture technologies have been developed in Yurimaguas (Peru) and Tamil Nadu (India) to provide the earthworms necessary for inoculation.

Culture of *P. corethrurus* at Yurimaguas (Peru) in the greenhouse

Pashanasi *et al.* (1992a) observed fast growth of *P. corethrurus* in the mixture of soil and sawdust used to grow seedlings of tropical fruit trees. This experiment indicated that the composted sawdust, a waste of the timber industry, might be used in the context of low-input agriculture as a food resource to produce large quantities of earthworms, and possibly sustain their activity in otherwise unsuitable soils (i.e. with C% = 1.5; N% = 0.11; Al saturation = 70%). Experiments have been done first in the laboratory to identify relative proportions of soil and sawdust that would optimize earthworm growth and reproduction. The following treatments were applied to identify the most efficient mixture:

- control soil;
- 75% soil; 25% sawdust by volume;
- 50 : 50 mixture;
- 100% sawdust;
- 25% soil; 75% sawdust;
- 75% soil; 25% sawdust + 20 p.p.m. inorganic P;
- 75% soil; 25% sawdust + 40 p.p.m. inorganic P;
- 75% soil; 25% sawdust + 60 p.p.m. inorganic P.

Inorganic P was added to some treatments to prevent phosphorus deficiency, a problem that may occur in earthworm cultures. Soil was taken from the upper 10 cm of a 20 year secondary forest. Sawdust was taken from a large pile outside the main sawmill at Yurimaguas. The residue had been deposited outside for at least 1 year and its dark colour revealed an advanced stage of composting. Sawdust is relatively rich in Ca, K and Mg, but is highly deficient in P and N.

Results indicated that *P. corethrurus* may grow and reproduce well in a mixture of soil and sawdust. Earthworms matured between 16 weeks (3 : 1 soil/sawdust) and 25 weeks (all other treatments except for pure sawdust and the 3 : 1 mixture with 60 p.p.m. P where the adult stage was never reached).

Maximum weights were observed in the 3 : 1 mixture with 40 p.p.m. P after 75 weeks. Minimum growth occurred in pure sawdust. Relatively high proportions of sawdust (1 : 1 mixture) seemed to be favourable to reproduction (206 cocoons produced within 75 weeks using an initial inoculum of 15 worms). The maximum mortality of worms (93.3%) occurred in pure sawdust, whereas the minimum of 27% mortality occurred in the 3 : 1 mixture with 60 p.p.m. P in 75 weeks. A 1 : 1 mixture by volume of soil and sawdust appeared to provide a low mortality (33.3% in 75 weeks), high cocoon production (206) and rapid growth (1204 mg on average at week 75). Addition of inorganic P improved the performance of earthworms, although differences were not significant.

On the basis of the above laboratory experiments, two types of earthworm cultures have been developed at Yurimaguas, i.e. (i) a small-scale nursery culture in wooden frames; and (ii) a large-scale culture in field bed culture.

Small-scale wooden frame earthworm culture technology developed at Yurimaguas (Peru)

Wooden frames 50 cm in length, 50 cm in width and 20 cm in height, closed at the bottom with a mosquito net wire mesh, have been used for laboratory cultures. Soil was taken from the upper 10 cm of a pasture soil. Sawdust was brought from a sawmill in the city of Yurimaguas where two species (i.e. the Melicaceae *Cedrela odorata* and *Swietenia macrophyla*) comprise most of the timber and boards that are produced. Soil and sawdust mixtures of 1 : 3, 1 : 1 and 3 : 1 have been tried. All the mixtures of soil and sawdust improved the growth of *P. corethrurus*, and the best result was obtained with a 3 : 1 soil : sawdust mixture. A moisture content of 36% equivalent to water content at field capacity was maintained in all sets. The wooden frames were kept in a cool and shady area. Forty earthworms weighing 20 g were introduced into each unit. The population reproduced rapidly and, after 1 month, more than 200 cocoons had been deposited (Fig. 7.2). One month later, an average population of 514.5 earthworms weighing 67.2 g fresh was found, which represents respective multiplication rates of 13.0 and 3.4 for numbers and biomass. Most individuals, however, were still immature and of a relatively small size (Table 7.2).

Large-scale bed earthworm culture technology developed at Yurimaguas (Peru)

To produce earthworms on a large scale, culture beds of 5 m × 1 m × 20 cm were installed in the field (Fig. 7.3) and filled with a 3 : 1 mixture of soil and partly composted sawdust, as was done for the wooden frame cultures. The beds were surrounded with nylon net to prevent escape of earthworms. No

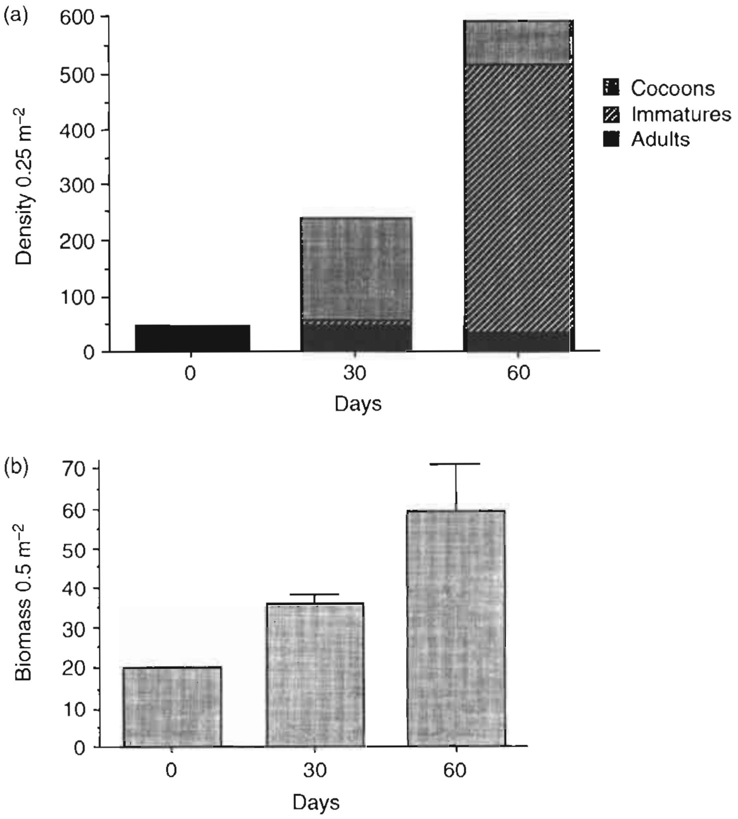

Fig. 7.2. Production of *Pontoscolex corethrurus* in wooden frames 50 × 50 × 15 cm in a 3 : 1 mixture of soil and sawdust (average of two replicates for each date). (a) Worm density; (b) production rate (estimated at 12,400 individuals (1.6 kg) m^{-2} year^{-1} and cost estimated as 7.8 Euro kg^{-1}; Table 7.1).

significant difference was observed between the sets with and without a net, indicating that when conditions are suitable earthworms do not tend to migrate. Initially, 20 *P. corethrurus* m^{-2} were inoculated in the bed culture. Another inoculation of 20 individuals m^{-2} was made after 40 days when it became evident that the initial inoculation was not sufficient (Fig. 7.4) (Pashanasi *et al.*, 1994). Thus, a total of 200 adult *P. corethrurus* weighing about 100 g live wt was later inoculated into all new units (Table 7.2). The cultures were maintained for 120 days. A total of 3355 worms weighing about 839 g live wt was harvested from each culture unit. Most earthworms were immature and still rather small.

Table 7.2. Technologies for production of soil-dwelling earthworms at Yurimaguas (Peru), and Carolyn and Sheikalmudi at Tamil Nadu (India).

	Yurimaguas (Peru)		Tamil Nadu (India)
	Wooden frames	Wooden log-lined bed	Vermiculture beds
Earthworm species	*Pontoscolex corethrurus*	*Pontoscolex corethrurus*	80% *P. corethrurus*, 20% *A. corticis* + native anecics
Size of units	50 cm × 50 cm × 20 cm	5 m × 1 m × 20 cm	6 m × 0.9 m × 55 cm
No. and biomass (g fresh mass) of adults inoculated	*40* 20	*200* 100	*1000* 450
Culture time (months)	2	4	3
Worm harvest per unit (*n* and g fresh mass)	*514. 5* 67. 2	*3355* 839	*15,000* 3750
Annual production (m^{-2}) *n* and kg fresh mass	*12,400* 1.6	*2000* 0.5	*11,100* 2. 8

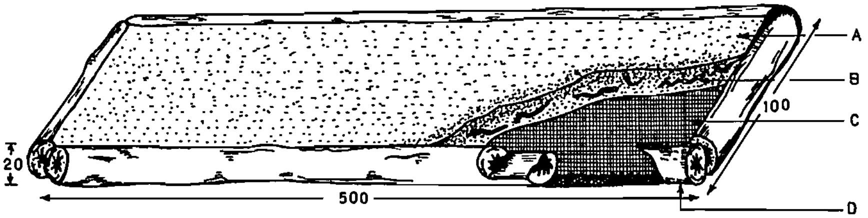

Fig. 7.3. A field unit for massive production of *Pontoscolex corethrurus* at Yurimaguas (Peru) . A, Soil and sawdust mixture (3 : 1 ratio); B, earthworm; C, mosquito net; D, wooden log. Dimensions are in centimetres.

Large-scale earthworm bed culture technology developed at Carolyn and Sheikalmudi (Tamil Nadu State, India)

Large-scale bed cultures have been developed close to field sites. Individual vermiculture units 6 m × 0.9 m × 55 cm depth were grouped into larger units of 26 beds at Carolyn and 20 beds at Sheikalmudi site of Tamil Nadu. Each bed was surrounded by a 2 foot pathway to allow access, and was surrounded by a side drain which ultimately led to the main drain to release excess water, especially in the monsoon period. The boundary of the vermiculture site was surrounded by shade trees. The culture site was covered by a galvanized wire frame supported by stone pillars. A layer of old sack cover/live creeper plant was provided to protect the cultures from high intensity solar radiation and rainfall (Fig. 7.5). Details of organic matter and the soil layout plan for preparation of the vermiculture bed and their justification have been given in the patent paper.

Soil moisture was maintained close to field capacity (15–20%) and soil temperature varied between 22 and 25°C at 30 cm of soil depth in the

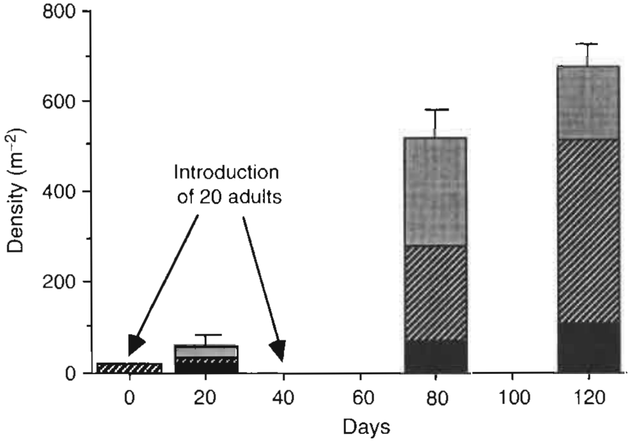

Fig. 7.4. Production of *Pontoscolex corethrurus* in a large-scale field culture in Yurimaguas (Peru).

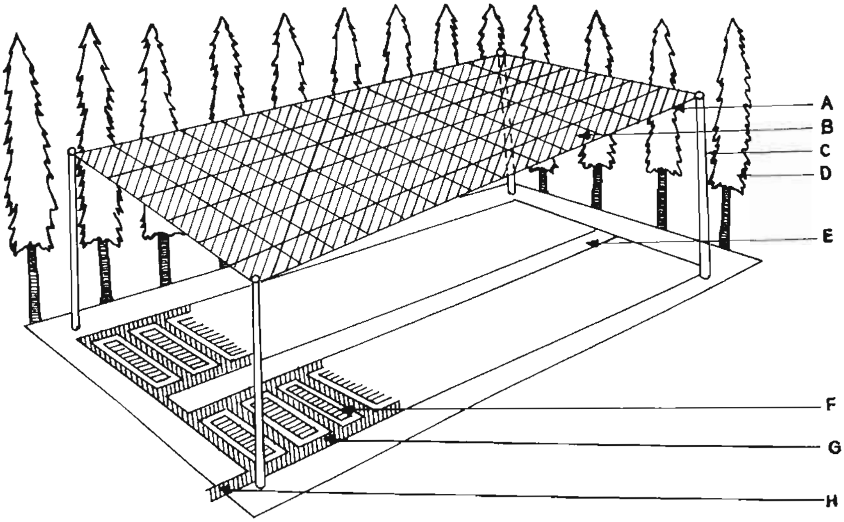

Fig. 7.5. Vermiculture plan layout to produce inoculum for in-soil technology. A, Galvanized iron wire; B, old sack cover; C, wooden/stone/iron pillar; D, shade tree; E, road; F, vermiculture bed; G, boundary drain; H, drain outlet.

vermiculture beds. *P. corethrurus* constituted approximately 80% of the culture, while other earthworms, e.g. *Megascolex konkanensis, Amynthas corticis* and *Metaphire houlleti*, constituted the rest of the population. This combination was determined by the initial proportions of earthworms existing in the field where there is need of earthworm application. Initial inoculation of 1000 adult and late immature worms to each vermiculture bed has resulted in production of about 15,000 assorted worms (Table 7.2, Fig. 7.6).

This amounts to about 185 individuals and 83.25 g live wt inoculated m^{-2} area of the vermiculture bed. The resulting cost of 1 kg of live *P. corethrurus* worms was 3.6 Euro when produced through large-scale bed culture (Table 7.3). Different levels of maintenance of on-farm bed culture in Tamil Nadu have shown that poor maintenance may result in about an 82% reduction in population density and biomass in comparison with properly maintained sites.

A comparison of wooden frame and bed culture has been made with respect to technology (Table 7.2) and cost of worm production (Table 7.3). Populations increased their density very rapidly in all situations, with multiplication rates of inoculum of 12.8, 15 and 16.5 after 2, 3 and 4 months, respectively, in small wooden frames and bed cultures in India and Peru. The multiplication rate of biomass calculated on a 1 year basis was 3.1 in wooden frames and 8.3 and 8.4, respectively, in bed cultures in Peru and India. These results indicate that although density increased very significantly in 2 months,

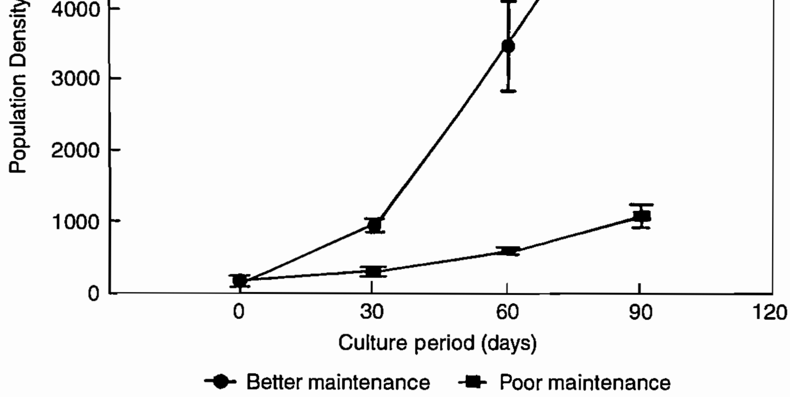

Fig. 7.6. Production of *Pontoscolex corethrurus* in a large-scale field culture in Tamil Nadu (India) at different levels of maintenance.

Table 7.3. Cost of production of endogeic earthworms at Yurimaguas (Peru) and at Tamil Nadu (India) sites.

	Yurimaguas (Peru)		Tamil Nadu (India)
	Wooden frames	Wooden log-lined bed	Vermiculture beds
Materials % (organic inputs + wooden frames)	16	9	44
Labour + maintenance%	31	34	37
Cost of inoculum%	53	57	19
Cost of production of 1 kg of live worms (Euro)	9.2	3.4	3.6

1 Euro = 1.1 US$.

it took 1 or 2 months more to obtain the subadult and adult worms that perform best in inoculations. Production in wooden frames had a 2.5-fold higher cost than the field method but had the advantage of occupying less space and being easier to control.

The cost of worm culture through different technology is comparatively less expensive by about 36% at Tamil Nadu and 79% at Yurimaguas for large-scale bed culture than collection from the field.

Development of Indirect Technologies

Effect of spatio-temporal management of crop rotations on earthworm communities at Carimagua (Colombia)

Soil macro-invertebrate communities

Savannas at Carimagua traditionally have been used for extensive cattle grazing. A long-term research project was conducted by Centro Internacional de Agricultura Tropical (CIAT) to find suitable and productive alternatives for sustainable land use based on rotations of annual crops with improved pastures (Thomas and Kevan, 1993). The aim of our specific research was to assess the impact on earthworm communities of experimented practices and identify spatio-temporal designs of rotation that would best sustain earthworm activities. Immediate objectives were: (i) to evaluate the diversity and ecological functions of earthworm species present in the area (see Chapters 1–3) and (ii) to describe the dynamics of the communities in time and space. Implementation of the latter objective has led to the design of new sampling techniques that allow collection of data sets that are suitable for geostatistical treatments (Rossi *et al.*, 1995, 1997). The total earthworm and macrofaunal biomasses at Carimagua show distinct variations with respect to land-use patterns (Decaëns *et al.*, 1994) (Fig. 7.7). The native savanna had the highest species richness (seven species). In the pasture–legume system, the same seven species were present and biomass had increased ten times, largely due to the response of *Martiodrilus carimaguensis*, a large anecic species (Jimenez *et al.*, 1998). Similar results had been observed already in a number of other tropical sites (Dash and Patra, 1977; Senapati, 1980; Senapati and Dash, 1981; Lavelle *et al.*, 1981). Improved pastures had the highest earthworm biomass, with a maximum value (41.2 g live wt m^{-2}), in a pasture consisting of the African grass *Brachiaria decumbens* and the herbaceous legume *Pueraria phaseoloides* ten times greater than in the original savanna.

In the rice monoculture, earthworm biomass was drastically reduced (1.86 g live weight m^{-2}) as in many tropical soils cropped to annual cultures (e.g. Lavelle and Pashanasi, 1989; Lavelle *et al.*, 1993; Panigrati, 1993; Senapati and Sahu, 1993; Senapati *et al.*, 1995; Mboukou-Kimbasta, 1997). This is largely due to soil tillage, reduction in soil organic matter returned to the soil and the application of pesticides (Domsch, 1970; Eijsackers and van de Bund, 1980; Austin, 1987; Austin and Smith, 1989; Woomer and Swift, 1994; Senapati *et al.*, 1994b; Giller *et al.*, 1997). There was an inverse relationship between termite and earthworm abundance, termites being more abundant in the native savanna and in cultivated plots where earthworm communities were reduced.

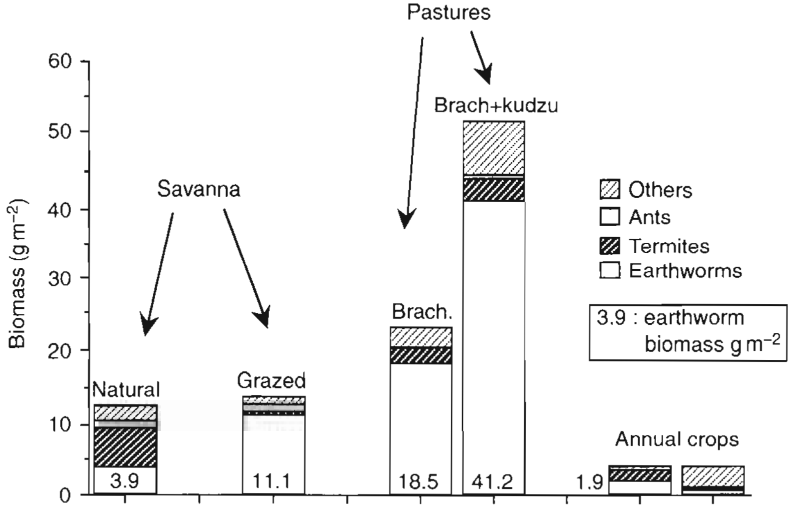

Fig. 7.7. Effect of land use on macrofaunal communities at Carimagua (Colombia).

Changes in earthworm spatial distribution

An experiment was started at Carimagua to test the effect of different crop and pasture rotations and their relative spatial layout on parameters of soil fertility and sustainability. The culticore experiment comprises ten different land-use systems organized in adjacent bands 20 or 40 m wide and 100 m long in a split plot design replicated four times (Fig. 7.8). Cropping systems under study were: (i) rice monoculture; (ii) rice–cowpea rotation; (iii) rice–green manure rotation; (iv) native savanna; (v) rice–pasture rotation; (vi) maize monoculture; (vii) maize–soya rotation; (viii) maize–green manure rotation; (ix) natural savanna; and (x) maize–rice–pasture rotation. In this design, it is possible to follow the spatial (i.e. local and across parcels) and temporal (i.e. across seasons and alternating type of land use) patterns of community dynamics.

A sampling was done using an experimental design consisting of 60–120 samples of 25 cm × 25 cm × 30 cm size, taken at every 5 m interval on regular square grids. Sampling done in 1995–1997 showed that populations of the main two species are distributed in subcircular patches about 20 m in diameter. This sampling showed that *M. carimaguansis* was able to build abundant populations in pastures and had low population densities in all cropped systems, although patches might be observed temporarily in cropped plots located close to a pasture. Avoiding tillage when populations are fully active seems to be an efficient way to prevent destruction of populations (Fig. 7.9).

Glossodrilus sikuani, a smaller size endogeic species (see Chapter 3), developed abundant populations in the 2-year pasture. In other systems, populations remained at a low level of abundance (Fig. 7.10). At the boundary between two different land-use systems with contrasting effects, patches did not seem to expand from the favourable to unfavourable systems.

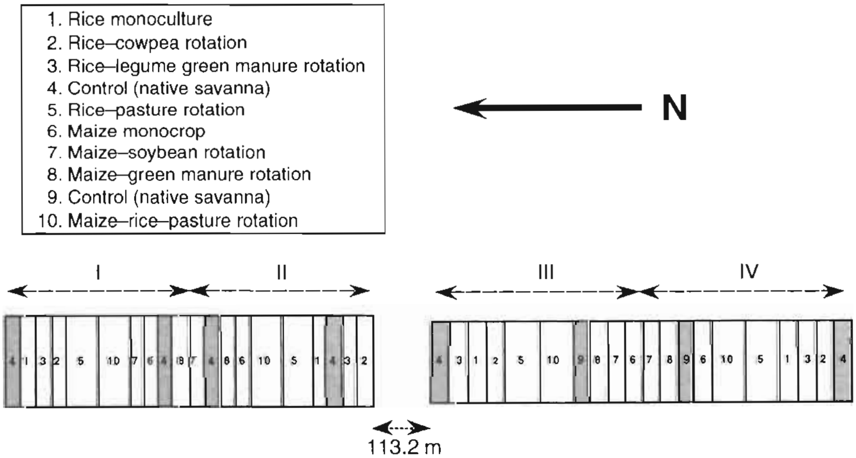

Fig. 7.8. Allocation of replicates and treatments into the Culticore experimental design at Carimagua (Colombia) (Thomas and Keiran, 1993).

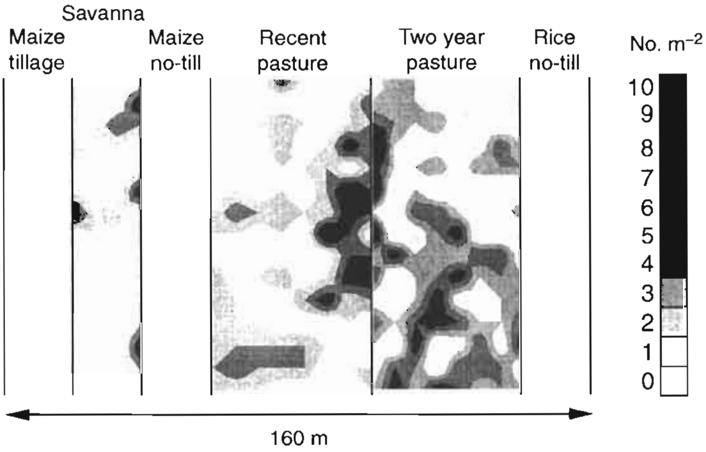

Fig. 7.9. Spatial distribution of *Martiodrilus carimaguensis* in the rainy season in the different plots of the CULTICORE experiment.

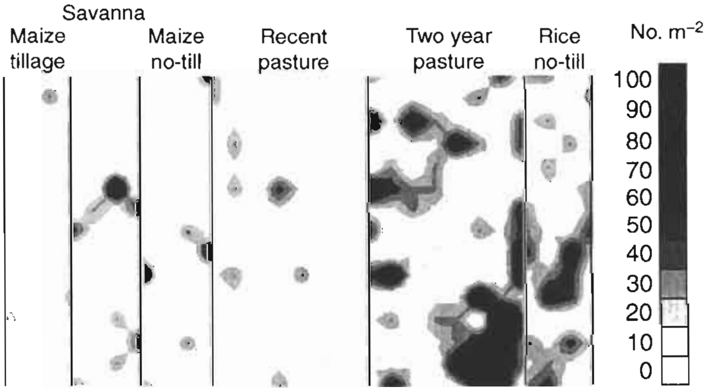

Fig. 7.10. Spatial distribution of *Glossodrilus sikuani* in the rainy season in the different plots of the CULTICORE experiment.

Therefore, the hypothesis of a colonization of earthworms from rich to poor systems is not supported. On the other hand, when two favourable systems were adjacent, there seemed to exist some continuity in the distribution of patches (see, for example, transition between rice and 2 year pasture for distribution of *M. carimaguensis*, Fig. 7.9). These observations showed that a proper management of soils may sustain and even increase earthworm activities when a natural ecosystem is converted to crops or pastures.

Direct In-soil Earthworm Technologies

Different techniques based on the inoculation of earthworms have been tested in our project. They comprise small-scale manipulations in nursery pots for tree seedlings, intensive horticulture plots of a few square metres and 0.5 ha plots of slash-and-burn agriculture at Yurimaguas (Peruvian Amazonia), 1 ha blocks in tea gardens of Southern India and restoration areas of Vertisols degraded by 15 years of intensive market gardening in Martinique. Earthworms (*P. corethrurus* and, occasionally, native species) were produced on site at Yurimaguas and at the two Indian locations; at St Anne (Martinique), *P. elongata* were collected manually from neighbouring pastures.

Development of direct technologies at Yurimaguas (Peru)

Experiments at Yurimaguas started in December 1989. Small-scale experiments were conducted to look into the effects of earthworms (*P. corethrurus*), crop residues (upland rice stubble) and legume green manure (*Centrosema macrocarpum*) on yield of various crops and soil fertility. Physico-chemical and biological parameters including plant production and decomposition kinetics of organic residues have been quantified and reported (Pashanasi *et al.*, 1992b, 1994; and Chapters 3–5). Crop production was sustained at the highest levels in the best treatments with high organic inputs and earthworm inoculation. The effect of earthworm inoculation was still observed at the fourth crop with a 50% higher grain production over no earthworm treatments. The incorporation of crop residue in the absence of earthworm inoculation resulted in a 38% increase in crop production in comparison with the control plot. Synergistic interaction of crop residue, legume green manure and earthworms resulted in enhancement of crop production by about 79.5% over the control (Pashanasi *et al.*, 1992b).

Enhancement of growth of tree seedlings by inoculation of earthworms in nursery bags at Yurimaguas (Peru)

Tree seedlings are highly responsive to the inoculation of *P. corethrurus* in nursery bags (see Chapter 4). At Yurimaguas, plastic bags were filled with a 1 : 3 mixture of composted sawdust and soil. Inoculation of ten young *P. corethrurus* in soil where tree seedlings were grown resulted in a significant increase in growth, especially with *Bixa orellana*, which grew 16 times better in 120 days and *Eugenia stipitata* (+150% growth), while *Bactris gasipaes* did not respond (Pashanasi *et al.*, 1992a). In the second phase of the Macrofauna programme, a similar technique was applied successfully to tea cutting culture resulting in a 220% increase in plant growth over a period of 6 months (Giri, 1995; see Chapter 4). An experiment was designed at Yurimaguas to test the hypothesis that such improvements were due to a higher rate of mycorrhizal infection (Ydrogo, 1994). Earthworm activities actually significantly increased this parameter in all cases. The highest rates of infection were observed with the highest levels of earthworm biomass, and with *B. orellana*, the tree species that was most responsive to earthworm effects. *B. gasipaes*, which is much less responsive, showed the lowest increase in mycorrhizal infection (Fig. 7.11). These results demonstrate that earthworms may have rather diverse effects on plants, which explains the variable responses that sometimes were observed. At Yurimaguas, *P. corethrurus* is now being inoculated systematically into nursery pots to stimulate growth of seedlings and mycorrhization in the field.

Development of horticulture techniques based on the joint use of composted sawdust and earthworms at Yurimaguas (Peru)

At Yurimaguas, in Peruvian Amazonia, 95% of vegetables consumed come from the Pacific Coast and San Martin region. Due to poor soil conditions, only native varieties can be produced locally, with low production rates and low prices, whereas the prices of good quality tomatoes vary between 0.6 and 1.8 Euro kg^{-1}. Local demand at Yurimaguas was 1300 kg per month in the market conditions of 1995. Limitations for market gardening production at Yurimaguas are mainly the low quality and acidity of soils close to the town, and scarcity of organic and mineral fertilizers. Experimentation has been implemented to try and establish a new technique based on the common use of sawdust as an organic resource and earthworms to stimulate nutrient release from sawdust and enhance plant growth.

At Yurimaguas, massive production of *P. corethrurus* was made on a 1 : 3 ratio mixture of composted sawdust : soil. Sawdust has high contents of nitrogen (3–4.7 g kg^{-1}), calcium (4.2–9.4 g kg^{-1}), magnesium

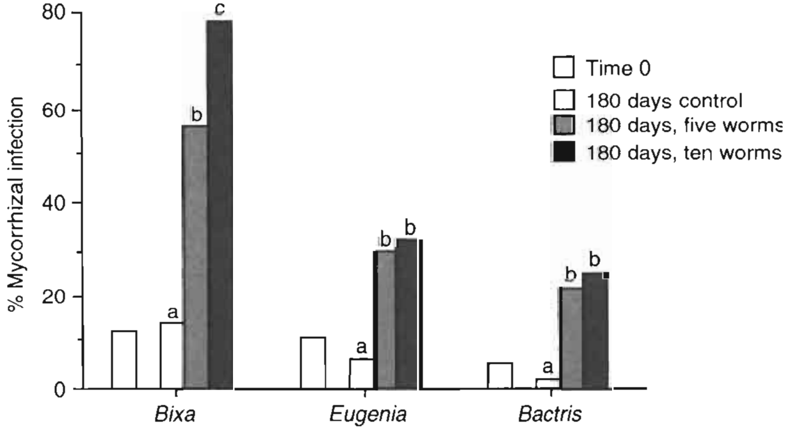

Fig. 7.11. Effect of inoculation of earthworms on mycorrhizal infection of three tree seedlings in the greenhouse at Yurimaguas.

(0.4–0.5 g kg^{-1}) and potassium (0.35–0.60 g kg^{-1}), but very low levels of phosphorus (0–0.29 g kg^{-1}). High proportions of lignin and polyphenols are considered limiting factors to nutrient mineralization. Analyses of the mixture after worms had been produced showed that aluminium toxicity was significantly decreased whereas concentrations of a few other essential nutrients such as calcium, magnesium and potassium were increased (Table 7.4). Preliminary experiments allowed the identification of tomato varieties that could grow in these conditions; a large tomato with high acceptance on the local market and, Perle, a very small tomato highly appreciated in developed countries as a snack, but rejected in Yurimaguas.

The first set of experiments was carried out with five treatments, two replicates of each treatment and 14 plants in each replicate. Production was low in most treatments. Production in a 1 : 3 mixture of sawdust and soil was twice as high as in the control soil, similar to a culture with a purely inorganic fertilization, but much lower than a conventional treatment with organic fertilization, and a treatment with organic and inorganic fertilization (Table 7.5). Differences in production may be attributed partly to the availability of nutrients in the diverse systems. Mortality of plants was high in all treatments due to unsolved problems of pests and diseases and to nutrient deficiencies.

Table 7.4. Chemical analysis of control soil and 1 : 3 by volume sawdust and soil mixture in vermiculture beds at Yurimaguas (mean of 12 different culture beds after 6 and 10 months of earthworm activity).

Time	pH	C (g kg^{-1} soil)	P (mg l^{-1})	Ca (cmol (+) l^{-1})	K (cmol (+) l^{-1})	Al (%)
Control soil	4.5	21.3	17.9	1.5	0.26	62.5
Six months	4.6	21.7	12.6	1.9	0.29	53.9
Ten months	4.2	25.4	15.5	2.9	0.28	47.3

Table 7.5. Production of tomatoes at Yurimaguas using different conventional treatments and an experimental earthworm technology.

Treatment	Yield (kg m^{-2})	% Mortality
Organic fertilizer 25 t ha^{-1}	1.43	25
Inorganic fertilizer NPK: 100–140–60	0.69	46
Organic fertilizer + NPK 50–70–30	2.77	11
Sawdust-soil 1:3 mixture + earthworms (200 m^{-2})	0.57	57
Control (soil)	0.29	57

Treatments with sawdust and worms had a relatively high mortality compared with other systems. New experiments have been started in which the system with sawdust and worms is supplemented with nutrients in organic (chicken slurry) and inorganic (inorganic fertilizer) forms to prevent any nutrient deficiency. The system that uses a mixture of organic and inorganic fertilizer is taken as control.

Large-scale on-farm experiments at Yurimaguas (Peru)

Most of the farmers at Yurimaguas practise traditional slash-and-burn cultivation systems. They clear and burn portions of the forest and then crop them to upland rice, maize or beans. After a brief period of two or three cropping cycles, fertility decreases and weeds invade the area. These portions are then abandoned as fallow land. Any practice that would increase sustainability beyond that short period of two cropping cycles and/or increase production would help to decrease the need to clear primary forest and significantly alleviate the task of farmers. Research at the experimental station 'San Ramon' at Yurimaguas had shown that application of fertilizers may partly solve the problem, but local constraints reduce the possibility to implement this technique effectively. Alternative methods are required that make better use of locally available resources (Sanchez *et al.*, 1982).

The experiment consisted of 12 plots with two treatments and three replicates in each plot (Fig. 7.12). In the middle of the plot, a strip of 0.4 m

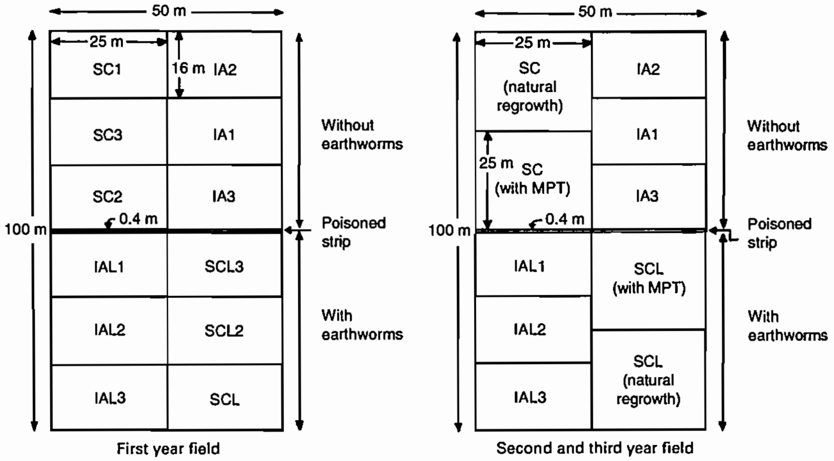

Fig. 7.12. Layout treatments for a first, second and third year field at Yurimaguas (Peru). L, earthworm (*P. corethrurus);* IA, improved agriculture with (L) and without earthworms; SC, shifting agriculture with (L) and without earthworms; MPT, multipurpose trees, replicates 1,2, and 3.

width and 50 m length was isolated by plastic sheets set vertically into the soil to 60 cm depth and treated with Furadan 4F (Carbofuradan 0.9 ml, l^{-1} of water) before each crop. This buffer strip was designed to prevent the movement of earthworms from the inoculated to the non-inoculated area. The secondary forest was slashed and burned manually, planted with rice as a first crop and interplanted with cassava after 2 months. After harvest, this area (shifting cultivation; SC) was abandoned to fallow. In half of the abandoned area, fallow was improved by planting some multipurpose trees (*Shaina* sp., *Inga edulis*) and the other half was left for natural regrowth. The improved agriculture treatment (IA) involved manual slash-and-burn preparation, and a yearly plant rotation of rice, cowpea and green manure (*Mucuna cochinensis*) sustained for 3 years. The major earthworm populations found in the plot were the three native species *Martiodrilus pano*, *Rhinodrilus lavellei* and *Rhinodrilus pashanasii*, together with *P. corethrurus*. Earthworm populations were sampled before and after the vegetation was burned. *P. corethrurus* obtained from large-scale bed culture (details given in this chapter) developed at Yurimaguas, Peru, were inoculated 15 days after planting the first crop in order to avoid death of earthworms due to high soil surface temperature. Inoculation of two *P. corethrurus* worms was made in the same hole where each seed had been planted 15 days before. A total of 17,500 worms was thus inoculated, i.e. 3300 in the SC and 14,200 in the IA plots at the onset of the experiment (Table 7.6). Inoculations were repeated twice in each treatment, and 62,000 worms were inoculated, presenting a biomass of 63.5 and 60.3 kg fresh mass, respectively, in the improved and traditional system.

Earthworm communities in the secondary forest had highly variable densities, with a minimum of 3 m^{-2} in SCL2 and a maximum of 62 in IAL1 and SC2. In the IA system, the parcels to inoculate already had a much higher biomass than the non-inoculated plot; the reverse situation was observed in the SC system. At the first harvest, populations of *M. pano* had totally

Table 7.6. Dates and amounts of earthworm inoculation (*Pontoscolex corethrurus*) on the two 1260 m^2 experimental plots at Yurimaguas.

Date	Improved agriculture	Traditional system
Jul 1993	12, 600 (10 m^{-2})	3,278 (2.6 m^{-2})
Dec 1993–Jan 1994	9,600 (7.7 m^{-2})	2,400 (1.9 m^{-2})
Jan 1995	9,600 (7.7 m^{-2})	
May 1995		24,600 (19.7 m^{-2})
Total	31,800 ~8 kg (63.5 kg ha^{-1})	30,278 ~7.6 kg (60.3 kg ha^{-1})
Cost of inoculation ha^{-1} (US$)	254	241

disappeared, but other forest species, especially *R. lavellei*, were still present. *Rhinodrilus pashanasii* populations increased in all situations (Fig. 7.13). This might have occurred due to high rainfall during the growing period and the use of surface residues after the slash-and-burn process. Introduction of *P. corethrurus* had no important effects on the overall density because juveniles of this worm need 3–4 months to become adults. Crop production was very uneven (Pashanasi *et al.*, 1992b, 1994). Earthworm biomass never reached 40–50 g fresh wt and the inoculum was probably insufficient to allow a rapid development of the earthworm population when the soil would have been still

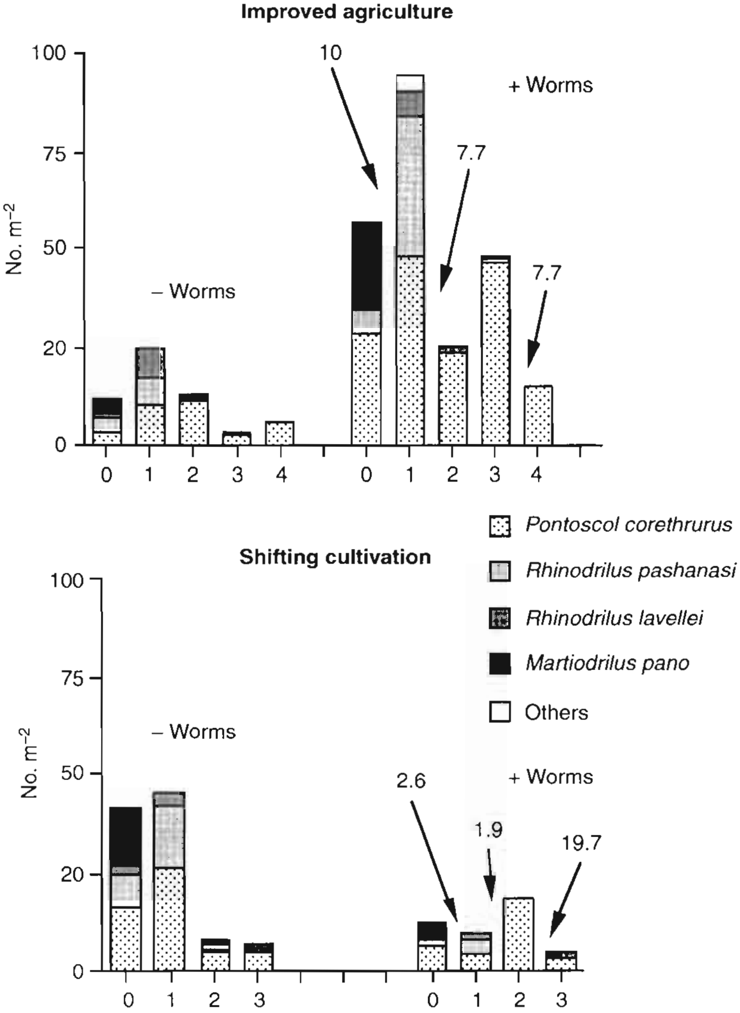

Fig. 7.13. Changes in the composition of earthworm communities in the two cropping systems during 3 years of experimentation (arrows indicate numbers of inoculated individuals).

favourable for their growth. The mode of inoculation (earthworms alone, with no soil) and the high proportion of juveniles in the inoculum (that would need at least 2–3 months before they would reproduce, and suffer mortality during this time) were factors responsible for this situation. Finally, the texture and fertility of soil appeared to be highly heterogeneous in the experimental plot; as a result, earthworm biomass was significantly greater in the non-inoculated control of the SC treatment than in the inoculated plot at all sampling dates.

There was no correlation between earthworm biomass at harvest and grain production. However, inside the SC treatments, correlation between crop yield and earthworm abundance at each sampling point was highly significant ($r = 0.78$, $P < 0.01$). Economic evaluation has been made on the first crop, and the costs of labour were 55 and 62.7% higher, respectively, in inoculated plots of SC and IA. As a result, the financial budget was negative in all treatments with earthworms (Pashanasi *et al.*, 1992b, 1994) (Table 7.7). No significant difference in any of the parameters monitored in this experiment was observed between inoculated and non-inoculated treatments.

The experiment failed because the initial inoculated biomass was too low and dispersed. In the unfavourable conditions of a slash-and-burn plot, populations could not multiply and their abundance remained at the initial level of inoculation. Another reason for the failure was that inoculated worms were mainly juveniles. Therefore, an initial inoculum of more than 300 kg ha^{-1} of adult worms seems to be necessary to provide efficient worm activity; as the cost of 1 kg fresh wt of worms is 3.4 Euro, inoculation of 1 ha would cost about 1000 Euro, a totally unrealistic investment in the economic context of these crops. An alternative may be to concentrate the inoculum in a small proportion of the area, within the reach of the roots, or to use techniques that stimulate the activity of local populations indirectly.

Table 7.7. Cost–benefit analysis of traditional slash-and-burn and improved agriculture with and without earthworm inoculation at Yurimaguas (Peru).

	Shifting culture		Improved agriculture	
	Non-inoculated	Inoculated	Non-inoculated	Inoculated
Incomes	3086	2137	1434	1222
Costs	923	2796	1289	4355
Benefits	2164	–479	145	–3134
Crops	Maize–cassava–fallow 12 months		Maize–rice–cowpea–rice 14 months	

Effect of earthworm inoculation in the restoration of a degraded vertisol by a pasture fallow at St Anne (Martinique)

In the south-east of Martinique, vertisols are usually cropped either to pastures (planted with *Digitaria decumbens*) or long-term intensive market gardening production. The latter practice has resulted in severe degradation through loss of organic matter, soil organisms and soil aggregate stability inducing soil erosion (Feller *et al.*, 1983) (Table 7.8).

In this degraded situation, the density of the existing dominant earthworm *P. elongata* is very low (2 m^{-2}) compared with the native pasture (90 m^{-2}) in Martinique. Pasture fallows may restore soil conditions in 5–10 years (Albrecht *et al.*, 1986). An experiment was conducted to evaluate the relative contribution of roots and earthworms to regeneration of degraded soils under pasture fallow. The aims of the study were: (i) to identify patterns of reconstitution of carbon stocks and recolonization by earthworms, and (ii) to test the effect on these processes of an early massive reinoculation of earthworms at the density of adjacent pastures.

A pasture was established at St Anne to restore the stocks of organic matter and, hence, the stability of the physical structure. This plot had been planted with *D. decumbens* 1 year before the onset of the experiment. Soil aggregate, carbon content, root biomass and earthworm abundance had been quantified for 3 years on a 0.5 ha plot at 178 sampling points randomly distributed on a regular square grid at 1 m intervals. This allowed the choice of three experimental plots 5 m × 10 m in size, located at places with equivalent carbon contents inside the 1 ha study field. Replicates were not possible due to the large amount of disturbance and elevated associated costs.

Table 7.8. Soil and biological properties of a Vertisol of south-east Martinique under long-term market gardening cultivation and long-term pastures.

		Market gardening	Pasture
Soil organic matter (t C ha^{-1})	0–20 cm stock	39	82
Soil loss under simulated rainfall (t ha^{-1})	150 mm h, 30 mn, ploughed surface	20.1	2.1
Root biomass (mg C g^{-1} soil)	> 500 μm (0–10 cm)	0.12	10
Microbial biomass (μg C g^{-1} soil)	0–10 cm	600	1200
Earthworm biomass (g m^{-2})	30 × 30 × 30 cm samples	3.1	336.4
Earthworm density (ind m^{-2})	30 × 30 × 30 cm samples	2	93.4

The three treatments were: (i) bare soil, no earthworms; (ii) plants only (*D. decumbens*); and (iii) a plot with both plants and earthworms (*P. elongata*, at a density of 90 m^{-2}). Vermicide carbofuran (1 kg 50 m^{-2}) was used under the trade mark name of Furadan 5G (5% active ingredient) to kill earthworms (Edwards, 1974; Thompson, 1974; Brown, 1978). In the experimental plot with earthworm inoculation, a trench of 30 cm width and 30 m length was dug out around the plot down to the bed rock. After excavating the soil, a thick plastic film was placed in the trench in a 'U' shape and soil was put back into this trench to prevent the escape of earthworms. A wire netting fence was installed around the experimental plots to prevent cattle from entering the field. Earthworms were collected from irrigated pastures where the population biomass may be as high as 4 t live wt ha^{-1} (Barois *et al.*, 1988). About 4500 live *P. elongata* worms were needed for the inoculation. To ensure a safe inoculation, earthworms were put in containers filled with soil, turned upside down and covered with mulch to avoid heating during introduction. A hundred such containers were evenly distributed at the surface of the plot. After 1 week, containers were removed and the contents were hand sorted for the presence of earthworms.

In the large plot, the carbon content in the 0–30 cm stratum averaged 14.1 mg g^{-1} soil at time zero but increased significantly to 16.6 mg g^{-1} soil after 4 years (Table 7.9). In the fourth year, the spatial distribution of carbon across the plot had regained the initial pattern of distribution (Fig. 7.14a). Low density of earthworms in Vertisols under intense market gardening (Barois *et al.*, 1988) had increased during the first year but decreased in the second

Table 7.9. Abundance of earthworms in the regeneration plot (density m^{-2}) and soil organic carbon content (mg C g^{-1} soil) (0–30 cm).

Time (years)	*Polypheretima elongata*	Cocoons *P. elongata*	Polyhumic endogeic sp1	Epiendogeic sp2	Total m^{-2}	C (mg g^{-1})
0	3.5	0.6	6.0	—	10.1	14.2
	(1.0)	(0.5)	(2.7)	—	(2.9)	(0.2)
1	5.6	3.7	20.1	—	29.3	14.3
	(1.6)	(1.2)	(7.2)	—	(7.5)	(0.2)
2	3.3	1.9	6.8	3.1	15.0	14.2
	(1.1)	(0.8)	(2.2)	(1.4)	(3.1)	(0.2)
3	8.6	4.8	43.0	19.7	76.1	16.7
	(1.9)	(1.4)	(11.1)	(4.7)	(14.0)	(0.3)
4	40.2	9.1	6.1	8.0	50.6	16.6
	(6.0)	(2.1)	(3.4)	(3.5)	(10.0)	(0.4)

sp1 small polyhumic endogeic species + newly hatched *P. elongata*; sp2 small epiendogeic species. Confidence limits are shown in parentheses.

year due to unfavourable moisture conditions during the sampling period, and increased again in the third year (Table 7.9).

Populations concentrated in patches about 20 m in diameter that developed from the edges of the plot and seemed to be interconnected (Fig. 7.14b). This pattern was apparent after 1 year. In the third year, a significant increase in carbon content and earthworm density was observed. However, a large part of the increase in density was represented by two small-sized species, one a small filiform polyhumic endogeic linked to the rhizosphere, and the other a small and slightly pigmented epi-endogeic. No spatial correspondence between increases in carbon and earthworm population were observed at that stage.

In the small experimental plots, the distribution in depth of carbon was different in treatments with earthworms: more carbon was found in the upper 10 cm and less below 30 cm (Fig. 7.15). The introduced population was maintained at a density and biomass much higher than in the non-inoculated plot, but still lower than in the adjacent permanent pasture (~90 m^{-2}) (Table 7.10). Part of the difference, however, may have been due to the relative inefficiency of the sampling method, since collection of individuals was limited to the upper 30 cm of soil. The experiment showed that in these soils, inoculation of an earthworm population equivalent to that of an old pasture is feasible. The carbon content in the soil was sufficient to sustain the biomass at a relatively high level, and reproduction occurred. There was no apparent effect of earthworm activities on overall accumulation of carbon, although depth distribution was modified in the third year. Regarding the impact on soil erodibility, plants clearly improved resistance to erosion. Earthworm-inoculated plots gave variable results, close to controls with no plants at the beginning (months 6 and 12), and similar to treatments with plants only after 18 months (Fig. 7.15). After 1 year, the root biomass sampled from a depth of 40 cm showed a maximum value of 15.4 g kg^{-1} dry soil) in the earthworm introduction plot, an intermediate value of 11.2 g kg^{-1} dry soil in the plot with only plants but no earthworms, and the lowest value of 3.3 g kg^{-1} dry soil in the plot where both worms and plants were eliminated. Only the differences between treatments with and without plants were significant.

Indirect and direct technologies in tea gardens at Carolyn and Sheikalmudi, Tamil Nadu (India)

Tea is a high value plantation crop in India. From an ecological viewpoint, it can be seen as one of the most important agroforestry systems maintained for more than 100 years (Banerjee, 1993). Production of tea was around 1000 kg ha^{-1} $year^{-1}$ during the 1950s and increased up to approximately 1800 kg ha^{-1} $year^{-1}$ between 1970 and 1985 due to the introduction of agrochemicals, after which production has almost stabilized. In the Anamallai and the Nilgiris tea gardens, Parry Agro Industries Ltd produce 3000 and 3500 kg ha^{-1} $year^{-1}$ respectively, but production is stabilized in spite of

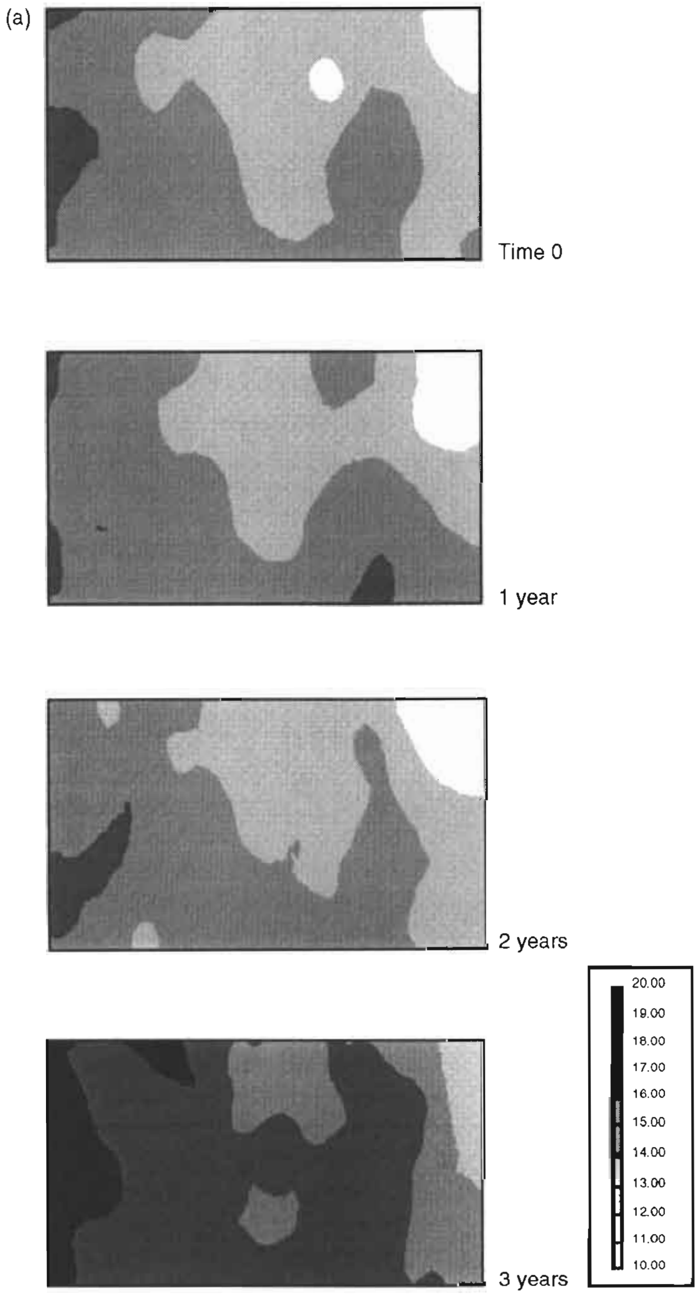

Fig. 7.14. Spatial distribution of (a) carbon content (% in upper 10 cm) and (b) earthworm density (m^{-2}) in the upper 30 cm of a 60 m × 140 m plot planted to *Digitaria decumbens* for 0, 1, 2 and 3 years after 15 years of continuous market gardening production.

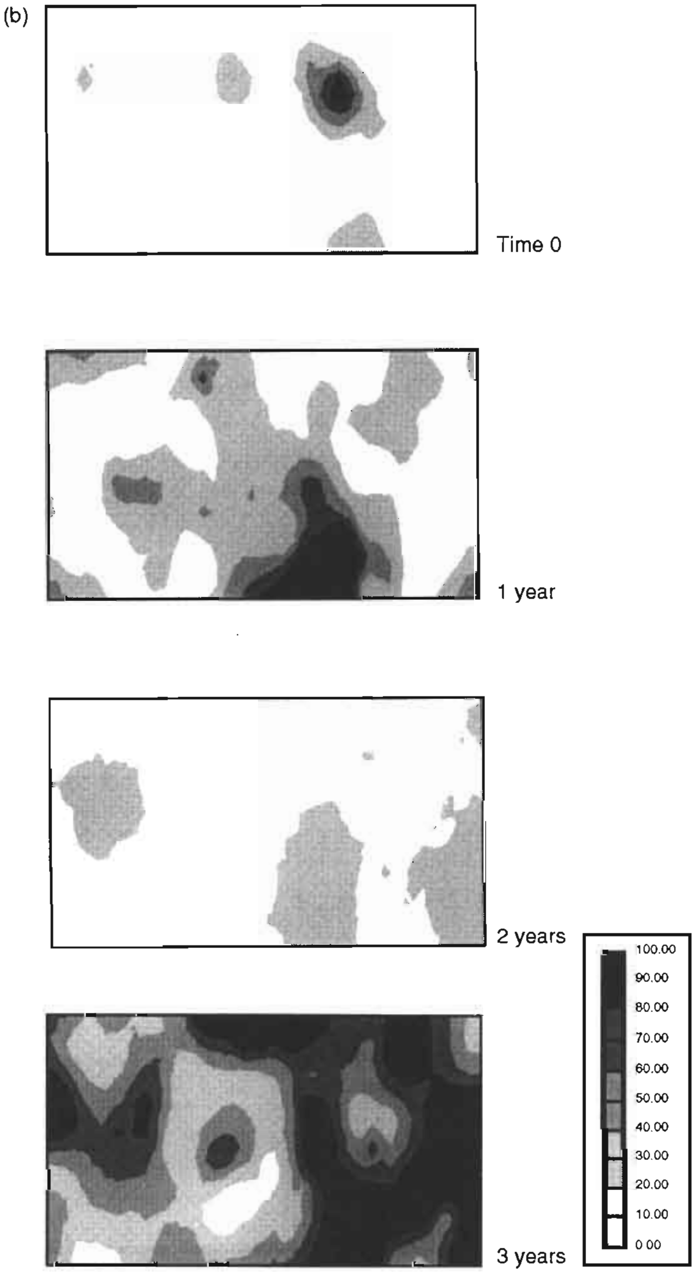

Fig. 7.14. *Continued.*

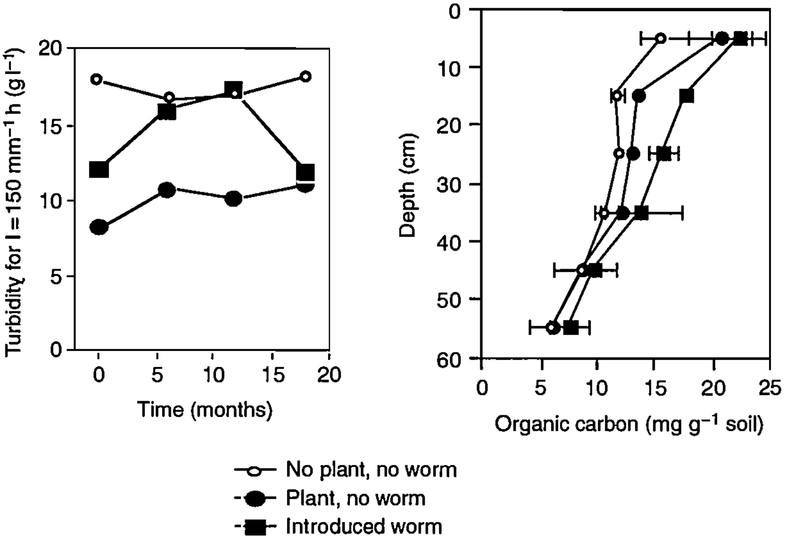

Fig. 7.15. Turbidity of runoff water after a 150 mm rainfall in 1 hour and distribution of carbon stock in the upper 60 cm of soil in the three treatments at St Anne (Martinique) after 2 years of experiment.

Table 7.10. Earthworm abundance in enclosures submitted to three specific treatments, and the large plot in process of natural regeneration.

	Control (bare soil)	Plants only	Plants + worms*	Natural regeneration
December 1994 (13 m)				
Biomass (g m^{-2})	0.05	0.07	35.7	6
s	0.08	0.13	38.4	10.4
Density (ind m^{-2})	4	4	48	43
s	6	6	34	74
June 1995 (19 m)				
Biomass (g m^{-2})	0.19	0.15	46.6	10.5
s	0.08	0.21	34.5	17.5
Density (ind m^{-2})	40	18	44	25
s	6	17	11	25

*Earthworms inoculated in November 1993, 90 ind m^{-2}; estimated biomass; 90 g m^{-2}.

continuously increased inputs of fertilizers and pesticides (Swaminathan, 1983; Beare *et al.*, 1997).

Preliminary studies indicated a significant depletion of soil faunal communities, especially litter-feeding epigeic and anecic earthworms of tea garden soil in comparison with the nearby forest. The excessive use of agrochemicals associated with problems such as compaction, leaching and soil erosion have actually eliminated 60–70% of the non-target organisms (Senapati *et al.*, 1994a, b). In tea gardens, native earthworm populations are most affected whereas proliferation of termites has been observed in some cases. As a result, the termite:earthworm ratio tends to increase in degraded soils and a negative correlation has been observed between this ratio and total yield ($r = -0.84$, $P < 0.01$). The long-term exploitation of soil has significantly affected some basic parameters of soil fertility such as water-holding capacity (WHC) (–11% compared with a nearby forest site), cation exchange capacity (CEC) (–29%) and organic matter content (–33%) in tea garden soil in comparison with the original forest soil (Senapati *et al.*, 1994b). Soil pH has decreased from 5.0 to 3.8, and aluminium saturation of the CEC subsequently increased from 10 to 60%. Soil of the tea garden also has a low calcium content and a high content of sesquioxides of aluminium and iron. Soil organic matter contents are correlated negatively ($r = -0.98$, $P < 0.001$) with the amount of agrochemical input.

Experiments have been conducted at Carolyn Estate (East division), Field No. 15 of Parry Agro Industries Ltd to test technologies that would indirectly, or directly, stimulate earthworm activities. Eight blocks, each of 1 ha containing 5000 tea bushes, located in the same field facing west were demarcated. Each block was isolated from the next by four rows of tea bushes serving as a buffer zone. Experimental units of 1 ha blocks were preferred by Parry Agro Industries Ltd to a classical split plot experimental design because: (i) technology developed on at least a 1 ha block could be adopted directly, and (ii) estimates of production of finished tea and qualitative assesment are usually done on areas of 1 ha. Special attention was paid to chosing blocks with similar soil and exposure conditions in order to produce significant results. The same design as repeated at another site (Sheikalmudi) with different soil conditions.

Treatments consisted of a control maintained under conventional technology (100% inorganic fertilizer inputs), four with different amounts, qualities and placement of organic inputs but no earthworm inoculation [i.e. 'organic' with 100% organic fertilization, mixed fertilization (50% organic), mixed fertilization with specific mechanical interventions ('trenching') and the same with incorporation of pruning material ('trench + inputs')] and two with earthworm inoculation, mixed organic and chemical fertilization, with or without incorporation of tree prunings ('trench + worms' and 'bio-organic fertilization'). The last treatment has been protected by a patent and all the experimental designs and technical layouts are detailed in the patent description. The effect of the first three treatments on tea production were assessed during nearly 7 years at Carolyn Estates; technologies involving mechanical operations and earthworm inoculations were tested during 5 years at two different sites (Fig. 7.16). Another experiment was established at another site for comparison.

Impact of high quality organic matter quantity

This experiment was designed to look into the impact on green leaf production and soil physico-chemical and biological components of replacement of respectively 50 or 100% of inorganic fertilizer with organic fertilizers providing an equivalent amount of mineral nitrogen. The inorganic fertilizer full dose was equivalent to 300 g N ha^{-1} as practised by Parry Agro Industries Ltd. High quality organic manure used in the experiment for 50 or 100% replacement of inorganic fertilizer was a commercially available brand prepared from processed city waste (Table 7.11).

Production in blocks fertilized with 50% organic inputs was respectively 37.6, 31.5 and 30.8% higher than in the block conventionally maintained during the first 3 years. In the following years, the difference decreased, due partly to the discontinuation of organic inputs for some time in 1995 and 1996 (Fig. 7.16). The average increase from 1992 to 1998 was 23%. Respective increases of 15.7, 17.1 and 12.6% (9% for the whole period) were observed during the same years in the block that received 100% organic inputs. ANOVA tests showed significant differences with respect to land

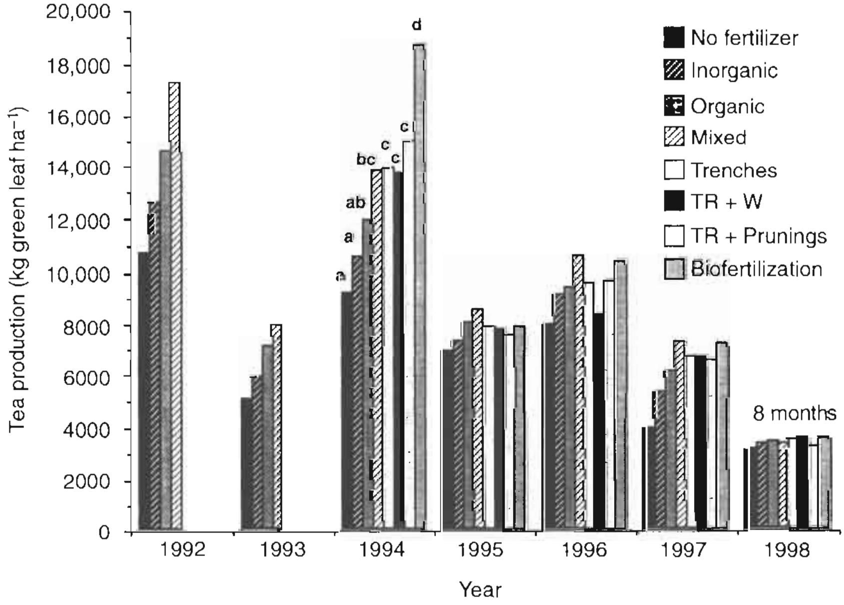

Fig. 7.16. Tea production at Carolyn Estate (Tamil Nadu, India) in plots submitted to different treatments (pruning occurred in 1993 and 1997).

Table 7.11. Chemical composition of Humigold.

pH	7.6
EC	0.34
C%	8.55
N%	0.67
$P(P_2O_5)$%	2.36
K_2O%	0.65
C : N	12.8

* Humigold is the commercial name of an organic manure prepared from city waste. Constituents are as per UPASI Tea Research Institute, Valparai , Tamil Nadu (India) analysis.

management alternatives (blocks). In the following years, differences were less marked. Cost–benefit analyses for 1992–1994 indicate 27.3–41.3% improvement in profit in the 50 : 50 inorganic : organic block and 10.3–18.9% improvement in the 100% organic block over the control block. The decrease in production observed in 1993 was due to pruning of the tea bushes, an event that occurs every 4 years.

Impact of trench incorporation

Trenching is an old practice that has been abandoned in plantation crops because of the increasing cost of human labour during conventional farming (Grice, 1977). Contour trenches with a 'lock and spill' quincuncial regular arrangement help to minimize soil loss and enhance production by about 12% in comparison with plots with no trenches (Padmanaban, 1975). This result is attributed to improved conditions of moisture and aeration. Trenches 1.2 m in length, 0.3 m in width and 0.45 m in depth were prepared between tea bushes in the experimental block in a lock and spill arrangement. About 3000 trenches were prepared in each 1 ha block and the impact of trench construction was studied. Of these 3000 trenches, 2000 were kept open with the excavated soil heaped on the lower edge to help in water harvesting, and the rest were filled with the excavated soil. This experiment served as a control for the next treatment where organic materials were incorporated into part of the trenches.

Trenching alone did not significantly enhance tea production in treatments that had received 50% of their N in an organic form (Fig. 7.16).

Impact of crop residue placement

Tea prunings, a low quality organic matter (Table 7.12), were buried in 1000 of the 3000 trenches made in experimental blocks where trenching had been done. The layout of different organic materials and other details have been

Table 7.12. Chemical composition of tea prunings (Natesan and Ranganathan, 1990).

	Mature leaf	Small stem	Thick wood
N%	3.20	1.37	1.04
P%	0.10	0.07	0.03
K%	1.24	1.00	0.55
Ca%	1.10	0.27	0.30
Mg%	0.17	0.09	0.06
Zn	1.75	2.05	2.25
Mn	48.9	17.7	12.8
Fe	13.8	30.2	16.4
Cu	6.6	13.6	4.2
Bo	1.8	1.2	0.6

described in patent papers. The total weight of the applied pruning material was about 12.5 kg m^{-2}. During the first year, results showed respective increases in production in comparison with conventional treatment, of +30.8 for treatment with 50% organic fertilization and surface application of prunings, and +42.3% when prunings were buried in trenches, although differences with plots receiving mixed fertilization were not significant. Corresponding increases in profit of 30.2 and 41.1% respectively were measured during the first year in comparison with conventional treatments.

The bio-organic fertilization technique

The bio-organic fertilization technique involves the use of organic fertilizers of low and high quality and earthworm inoculation following rather specific spatio-temporal patterns. This technique has proved very successful at Carolyn Estate, where tea production increased by 79.5% in comparison with a control plot receiving 50% fertilization as organic material. During the first year of application (1994), the bio-organic fertilization technique was significantly more productive than all the other techniques. For the period 1994–1998 (Table 7.13), differences in production between the biofertilization, and mixed fertilization techniques were not significant. Significant differences were observed with the unfertilized control plots receiving purely organic, or inorganic fertilization, and plots that had been submitted to trenching and earthworm inoculation, with no addition of prunings. This probably means that the biofertilization technique only stimulates production for some time and that organic materials and earthworms should be reinoculated at every pruning event. These two techniques, however, had significantly higher productions than the no fertilization, 100% inorganic and 100% organic

Table 7.13. Comparison of monthly values of tea production using different treatments from 1994 to 1998 at Carolyn Estate (Fisher's PLSD test).

	No fertilizer	Inorganic	Organic	Mixed	Trenches	Trenches + prunings	Trenches + worms	Bio-organic fertilization
No fertilizer		0.35	0.09	0.04*	0.02*	0.009*	0.06	0.0001*
Inorganic			0.44	0.05*	0.16	0.09	0.35	0.001*
Organic				0.24	0.52	0.36	0.88	0.01*
Mixed					0.59	0.79	0.30	0.20
Trenches						0.78	0.63	0.07
Trenches + prunings							0.44	0.12
Trenches + worms								0.02*

*Difference significant at $P < 0.05$.

fertilization techniques, respectively. Encouraged by these first experimental results, Parry Agro tested the technology at Lower Sheikalmudi, another site with different soil and climate conditions, where management of tea plantation is identical. Production was enhanced by 276% during the first year, and profit increased by 282% (Fig. 7.17). Large areas have been managed since then using the technology, and results confirm the trend observed during the first year following installation. At present, 80 ha year^{-1} are being treated with the technique, and over 20 million worms are produced yearly (Panigrahi, personal communication).

A patent was deposited in 1996 in Sri Lanka ('Fertilisation Bio-organique dans les Plantations Arborées' 4/9/96 at Colombo, Ref. No. 11034) and internationally (ref. PCT/FR 97/01363) to protect the technology. It has been extended since to several countries. All the technical details and procedures for operation are described in the patent document.

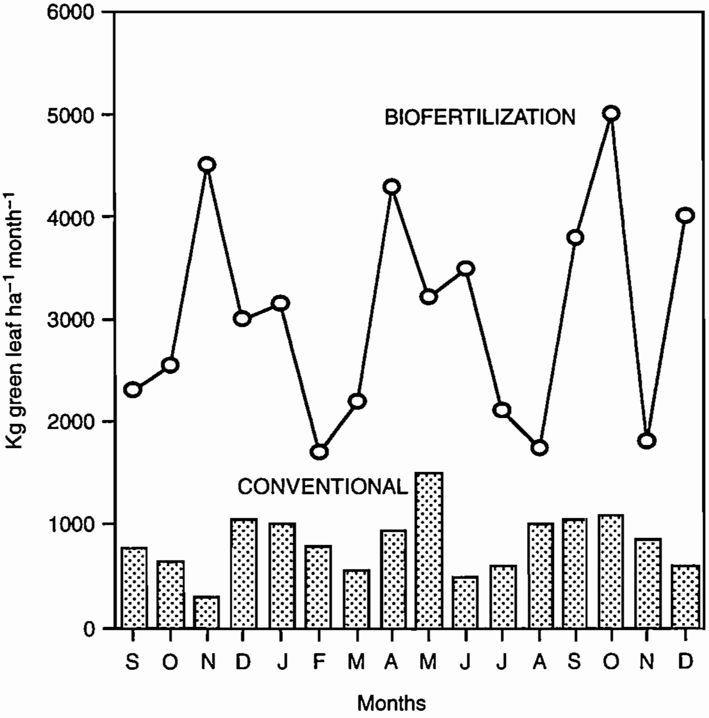

Fig. 7.17. Tea production at Sheikalmudi Estate (Tamil Nadu, India) in 1995, in plots managed with three different technologies.

Conclusions

Soil faunal communities and especially earthworms are negatively affected in most annual and some perennial cropping systems. Short-term and long-term earthworm inoculation experiments in different countries have indicated that management of organic matter and earthworms may significantly enhance plant production and profit (see Chapter 4). The bio-organic fertilization technique that allowed increases in tea production of 79.5–276% and of profit from 75.9–282%, respectively, in the first year following installation is a good example of the success of this approach in wealthy agricultural systems. This technique should be applied every time the high value of crops justifies it; this involves tree crop plantations in the tropics, and suburban horticulture where the shortage of land makes intensification of production necessary, and earthworm activities allow the use of low quality organic wastes as fertilizer. Remediation of degraded ecosystems might also benefit from these techniques, where earthworm activities may considerably accelerate soil formation and enhance production of pioneer trees used to recreate an ecosystem. More research is needed to consolidate and expand the technical knowledge elaborated in this project and in others.

However, the cost of earthworm production and inoculation (e.g. 5.5 Euro kg^{-1} fresh wt, i.e. at least 1500–2000 Euro to have a significant inoculum on a 1 ha base) is such that, in many cases, indirect stimulation of earthworm communities will be the only way to take advantage of their beneficial activities. This consists mainly of improving organic inputs through the use of suitable perennial plants when possible, or via organic inputs. Yet, it is still impossible to relate the amount of organic inputs of determined quality(ies) and the diversity and abundance of the soil macrofauna that will be sustained with these inputs.

Experiments at Carimagua suggest that the spatial and temporal array of parcels allocated to different crops may favour the conservation of locally high earthworm population density and diversity; these spots may serve as reservoirs and refuges for colonization of depopulated areas. However, much research is still necessary to produce simulation models and technical procedures that conceptualize these issues and result in applicable techniques.

Among the other important questions still not answered are the level of biomass that is required, the value of maintaining biodiversity in the managed communities, and the ways to achieve this purpose. Our results have shown that only a few earthworm species, mainly peregrine 'exotics', are susceptible to direct management. It has been proved recently that, under specific conditions of mismanagement of pastures in Central Amazonia, *P. corethrurus*, an exotic species that enhances the growth of most of the plants that have been tested, may behave like an 'invasive species', occupying niches made empty by deforestation and severely compacting the soil, with immediate negative effects on plant production and soil properties (Chauvel *et al.*, 1999).

The use of direct technologies such as the bio-organic fertilization technique, when it becomes widely used, will raise problems linked to the shift from the local to regional scale. Conflicts of interests possibly will occur due to the use of organic resources of different qualities, and space necessary for the production of the large amounts of earthworms required, at least in the early stages of the technical shift. As a result, while technical progress gradually improves techniques that favour earthworm activities, socioeconomic research will be needed to prepare the ground for their wide acceptance and optimal use.

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8

Perception and Use of Earthworms in Tropical Farming Systems

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Summary

An ethnological survey of knowledge of earthworms was carried out in four tropical countries (Mexico, Peru, India and Congo). A total of 202 farmers from 20 localities were interviewed to clarify their perception of soil fertility and its relationship to earthworm activity. Four additional farmers' meetings supported the results of these inquiries. In Peru and India, most of the farmers recognized a beneficial effect of earthworms, whereas in Congo and Mexico lack of knowledge predominated. In this last country, sampling was more intensive, covered three different ethnic groups and revealed an interesting inter-ethnic variability. In America, empirical knowledge and myths recognized an important role of earthworms in soil fertility. It is concluded that management practices focused on increasing earthworm populations will be accepted by local farmers. In some situations, however, an educational programme will be necessary.

Introduction

The results presented in the early chapters of this book clearly indicate that earthworms of tropical agroecosystems (natives and exotics) increase soil fertility and that management is possible either by direct or indirect manipulation. The latter refers to the development of agricultural practices that protect

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(eds P. Lavelle, L. Brussaard and P. Hendrix)

and/or enhance earthworm populations. However, adoption of new agricultural practices by indigenous farmers is not a simple task. The way they manage their crops is the result of hundreds (if not thousands) of years of empirical knowledge transmitted by word of mouth from one generation to the next (Kloppenburg, 1991; Toledo, 1995). As this knowledge is a mixture of beliefs, superstitions and practical experience, ethnological research should be carried out to guarantee that a new practice will be accepted. Examination of a few different practices across three continents and 28 tropical countries showed that annual low-input systems have detrimental effects on worms (Lavelle *et al.*, 1994). The Maala system in Congo (M'Boukou, 1997) and Totonac managment in Mexico (Ortiz-Espejel, 1997) are interesting agroecosystems in which earthworm communities are maintained systematically.

This chapter is an ethnoecological exploration of the world of perceptions, beliefs, attitudes and uses of earthworms by peasants in different countries of America, Africa and Asia. From a social point of view, it can be considered as an ethnobiological approach to sustainable soil management. We agree with other authors that only with economic and socio-cultural knowledge can the efficiency of the use of soil resources be improved (Swift *et al.*, 1994).

The ethnological approach

Human groups, through centuries of biological and cultural evolution (Klee, 1980), have built up different images of nature. The intensity of this interaction is a direct response to a given economic production system (Toledo, 1995). Once this aspect was recognized, several scientific disciplines related to rural development began to study the cultural foundations of traditional agroecosystems (Myer, 1998). As a result, several common patterns were found in most of these systems, which actually include polycultivation, ecogeographical diversity and use of small land parcels (Altieri, 1995; Bocco and Toledo, 1997).

As Altieri (1992) has pointed out, a better understanding of nature will be obtained only by mixing naive and scientific knowledge. For example, some of the ecological generalizations currently used in modern sustainable agriculture (e.g. polycultures) have been derived from traditional agroecosystem knowledge (Wolf, 1986). Thus, before new alternatives to rural development are proposed to farmers, scientists should try to understand how these groups manage their lands. We know that, in general, there are two complementary strategies of indigenous agricultural practices: those which burn vegetation (slash-and-burn practices of American farmers) and those that use organic wastes as mulching (e.g. the Maala systems of Congo). What we do not know is the perception that these farmers have of soil fertility in relation to earthworms.

Methods

Two approaches were used in this study: (i) a general inquiry involving 202 families to assess farmers' knowledge, and (ii) interactive workshops with farmers to compare and discuss beliefs and traditional knowledge.

In the first case, a questionnaire was designed for that purpose (Appendix 8.1) and applied to farmers from Mexico (north, central and south of Veracruz State), Peru (Yurimaguas), India (Yarpadi) and Congo (Niari Valley). The main objective was to evaluate the cultural acceptance by farmers of earthworm management by exploring their socioeconomic environment, together with their knowledge, attitude and conceptions about earthworms and soil fertility. All the socioeconomic, agronomic and ethnobiological data were stored in a database file directly linked to other EWDBASE files. Questionnaires were applied between August 1993 and July 1996. Table 8.1 shows the number of localities and farmers interviewed for each country.

In the second case, four farmers' meetings were carried out in Mexico during the period 1992–1995. The objective of the first three meetings was to explain to local promoters our conceptions about soil fertility and how to apply the questionnaire to interviewees. By using local promoters, we were confident that answers to the questionnaire were not biased. The last and most important meeting was held in March 1995, where three indigenous groups from different regions of eastern Mexico discussed their conceptions of soil fertility and earthworm roles.

Results

General patterns

The 202 questionnaries applied produced more than 10,000 specific data points stored in EWSOCEC (Dbase IV). In general, socioeconomic data showed that almost all interviewed peasants were low-input farmers for whom optimization of photosynthesis, natural precipitations and animal and human labour forces were the main energy inputs to crops.

Table 8.1. Socioeconomic and ethnological activities carried out in different tropical countries.

	Mexico	Peru	India	Congo	Martinique
No. of localities	16	2	1	1	1
No. of farmers	163	7	20	12	3
Farmers' meetings	4	0	0	0	0

The earthworm knowledge of indigenous farmers varied from country to country (Fig. 8.1) and even from region to region. In Peru and India, more than half of the farmers interviewed considered earthworms as organisms beneficial to the soil. In Congo, female farmers revealed a complete lack of knowledge of earthworms and showed an attitude of displeasure towards these organisms. In these three countries, there were no farmers that considered earthworms as harmful soil organisms. In Mexico, on the other hand, a lack of earthworm knowledge dominated (54%). Although 34% of farmers considered them as beneficial, in contrast with the others countries, more than 10% of Mexican farmers considered earthworms to have a harmful role.

Such a varied response by Mexican farmers was due to regional and gender variation (Fig. 8.2), a situation expected to be in other countries once more farmers are interviewed. However, it was surprising that in the Congo so many farmers were totally unaware of earthworms, when in reality these farmers have developed a special kind of crop fertilization that increases the biomass of earthworms.

Regional variation in southeastern Mexico

Three different ethnic groups inhabit the state of Veracruz in Mexico: Totonacos in the north, Nahuas in the centre and Zoques-Popolucas in the south. Their attitudes towards earthworms were varied (Fig. 8.3). Whereas the northern and southern groups (92 and 26 farmers, respectively) were very similar in their attitudes (34% of them recognized a beneficial effect and 55%

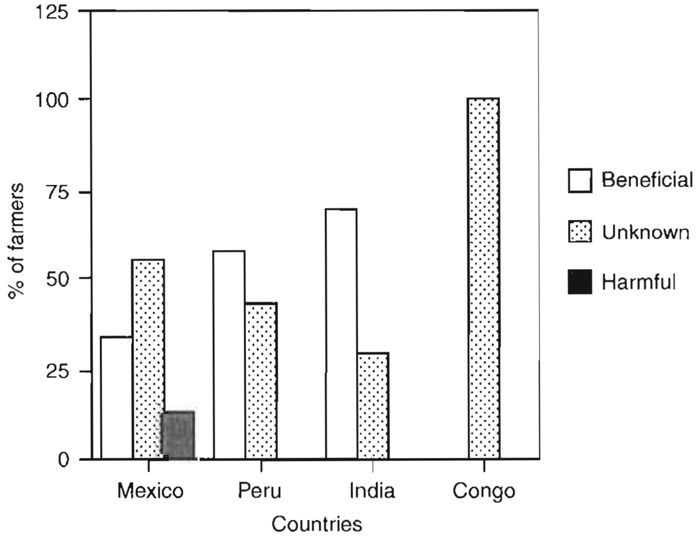

Fig. 8.1. Farmers attitudes towards earthworms in different tropical countries.

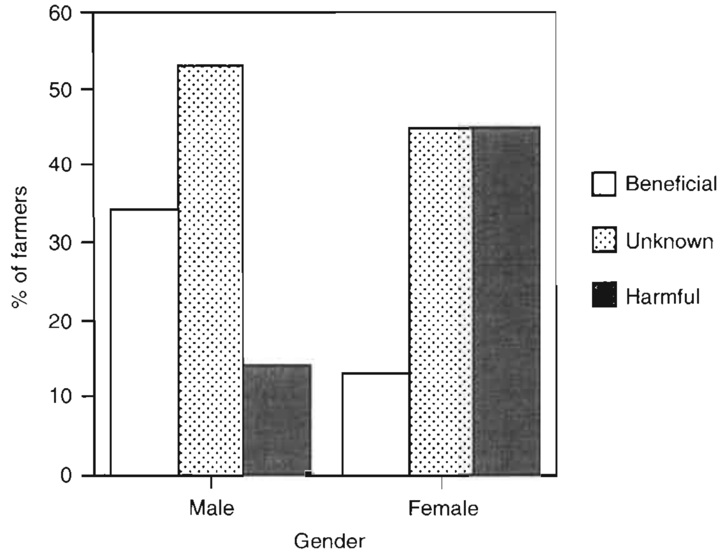

Fig. 8.2. Influence of gender on the perception of the role of earthworms in soil of indigenous farmers of eastern Mexico.

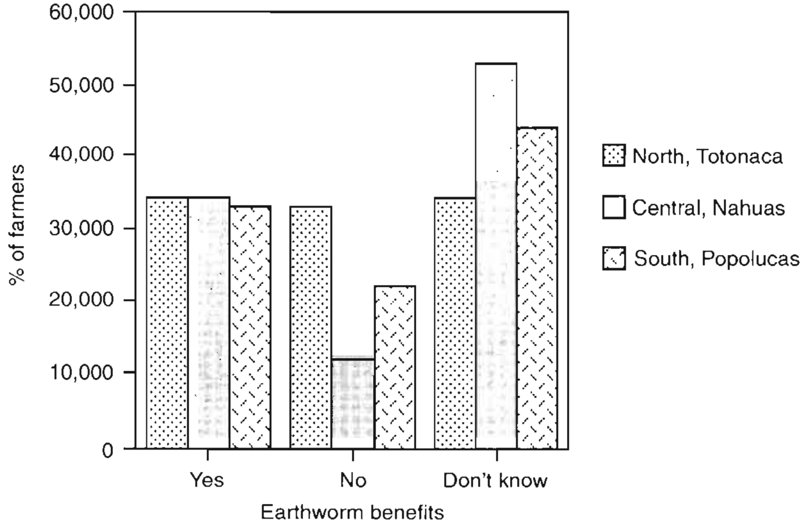

Fig. 8.3. Perception of the benefical effects of earthworms in cultivated soils of Veracruz, Mexico.

were ignorant), the centre group (44 farmers) was characterized by a more negative attitude since 22% of interviewed farmers considered earthworms unimportant or even harmful for the soil.

Traditional knowledge, myths and beliefs about earthworms

Traditional knowledge

In the four countries where the survey took place, farmers recognized the existence of three or four types of earthworms on the basis of size, colour and habitat. However, it was in Mexico where this knowledge was recorded in more detail. This was due mainly to the farmers' meetings, where 28 farmers and promoters from the three regions in which the survey was conducted discussed their opinions in depth. The dynamics of this workshop were based on the principles of exchange of information among participants (scientist–farmers and farmers–farmers).

It was therefore possible to obtain a traditional earthworm taxonomy from the three ethnic groups (Table 8.2). This is possibly the first report in the literature. This folk taxonomy for earthworms did not correspond to a scientific classification, because farmers considered different species under the same name (even from different origins: natives and exotics). The criteria used in the classification were colour, form and habitat, although these varied within each social group.

Farmers' knowledge of earthworms in Mexico is referenced in a book written in the 16th century by Martin de la Cruz entitled: *Libellus Of*

Table 8.2. Equivalence of earthworm knowledge between different southeastern Mexican indigenous groups and the western equivalent.

	Ethnic group		
English names	Totonacos	Nahuas	Popolucas
Earthworm	xpaluwa tiyat	tlalocuilin	toth
From within	xpa		
Worm	luwa	ocuilin	
Earth	tiyat	tlal	
Crop earthworm	xpaluwa katashawat		
Litter earthworm	xpaluwa tzozoco		
Orchard earthworm	xpaluwa kiljti		
Pasture earthworm		piitsaj	tlalocuilin
Sandy soil earthworm		xallalli	tlalocuilin
Swamp earthworm	bek tlalocuili	tuhuz toth	wuhiipiihnii
Yellow soil earthworm		tuhuz toth	puuhchnas
Red-neck earthworm	kechilti	tlalocuilin	
Black earthworm		tuhuz toth	yiknas

Medicinalibus Indorun Herbis (Folio 9V. Trad. 157) where the use of earthworms as healing agents of human cranium fractures is mentioned. Likewise, in the Florentin Codice (book 11 paragraph 13), eight different classes of worms are mentioned, including earthworms (tlalocuilin). We found no more information on the use of these organisms, and in general it can be said that in Mesoamerican literature there are very few written references on this topic (López Austin, personal communication)

Uses

In the Nahuas region (Zonglican Mountains, Veracruz), we recorded the existence of a medical practice that uses earthworms as spermaticides, as has been reported recently in China (Zhang *et al.*, 1992). Briefly, this practice considers that if a woman has sexual relations in the 40 days after giving birth, she must be cleaned with a medical preparation to avoid a worm infestation. After washing with arnica (*Zexmenia pringeli*, Greenm) water and itskuinyekatsolxiuitl (a wild herb, no identity) and dried off with clean cloth, the cervix should be impregnated with a previously heated oil solution (a mixture of bull fat, cochinimmas and earthworms, (preferently the red ones); the operation is repeated for 15 consecutive days, during which she must bathe in the Temaxcal. A temazcal is a small construction next to the house in which people take a steam bath (Isabel Ixatlahuac, Sierra de Zongoica, Veracruz, personal communication).

Beliefs

In the same region of Zongolica, people believe that feeding newborn children earthworms will preclude any sexual deviations in their subsequent development; children must be fed earthworms whose first and last seven segments have been removed (Isabel Montalvo Sierra de Zongolica, Veracruz, personal communication).

The following oral traditions about earthworms were also recorded in the Totonaca region of Papantla, Veracruz (Domingo Francisco Velazco, Fransico Sarabia, Papantla, Veracruz, personal communication):

- According to the belief of the Totonaca people, it is said that the earth organism is similar to the human organism and that earthworms are like the worms that live in the gut of man. Therefore, the earthworms are the world's gut that purify the earth. If earthworms die, the soil is lost.
- Men always have the queen worm (Xa tse Luwa) the one which helps to purify ingested food while eating; if that worm is expelled, the person could get sick and even die because there will be nothing to purify the food.
- When earth is given a personal status, there is the belief that worms live in the organism of earth and that they should live there to purify their organism and thus the earth will have good life and will provide good life to all of us that live on her.

In the same way, among Papantla farmers, there is a clear idea that earthworms are geophagous and that their excrement fertilizes the earth (Gerardo de la Cruz, Plan de Hidalgo, Papantla, Veracruz, personal communication). These beliefs correspond to what Aristotle said about earthworms, that they are the 'earth's intestines'.

Finally, by living within the soil, earthworms are considered 'daughters of Tlalocan' lord of the Earth (Nahuas from Mexico) or 'Cuica Mama' (Quechuas from Peru). They are placed in the upper levels of the terrestrial incarnations of superior forces that protect animals and plants (Heyden and Bauz, 1990). To Nahua people, therefore, they are considered the 'minor assistants' of Tlalocan, those that make vegetation grow and that maintain soil humidity (Manuel Orea, Zongolica, Veracruz, personal communication).

In summary, it is possible to recognize that rural knowledge (traced back to prehispanic roots) on the classification of earthworms and a valuation of their positive effects on annual crops exists among some Mexican indigenous groups. It could be said that for these groups earthworms constitute a symbolic bridge of fertility and health between man and nature.

Discussion

Recognition of the role of earthworms in soil fertility dates back to Egyptian and Greek times, when Aristotle mentioned their importance. More recently, Gilbert White (1789, quoted in Bouché, 1972) also considered earthworms to be the main promoters of vegetation, whereas Darwin's book (1881) constituted the first serious attempt to measure and evaluate the role of these organisms. In the first half of the 20th century, diverse investigations confirmed the important role that earthworm communities have had in soil formation as well as in the maintenance of its agricultural fertility. Perhaps the most outstanding statement comes from the US Department of Agriculture which stated in a 1949 report that: 'The investigations carried out in the Nile River Valley in the Sudan indicate that the great fertility of these soils is mainly due to the activity of earthworms. The observations and records carried out indicate that earthworm casting production during the activity period reaches values of 120 tons/acre/year' (Voison, 1974).

In spite of these antecedents, during the second half of this century soil fertility relied on external inputs more than on their inner biological components. As a consequence, traditional agricultural practices and knowledge of soil biota were overlooked.

As an illustrative example, traditional soil classifications were abandoned until recently when attempts have been made to recover this information. In Mexico, for example, this knowledge goes back to prehispanic time (Gibson, 1964) using a nomenclatural characterization of lands, whereas Williams (1977) indicated the existence of 45 classes of soils including those for both administrative and management purposes. Similarly, other ethnoedaphic

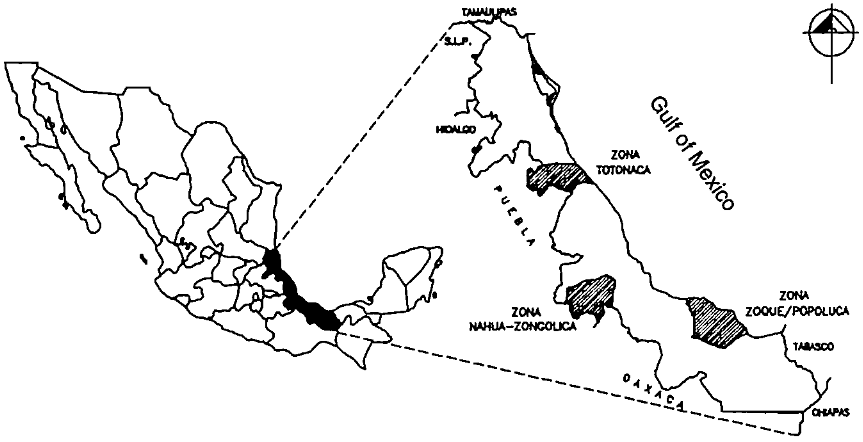

Fig. 8.4. Ethnological regions studied in Veracruz, Mexico.

researches (Barrera, 1988) have recognized that among indigenous Mexican peasants, soils are as important as other natural elements since they are 'all things sustaining'. From a classification point of view, the soils among the indigenous groups of Mesoamerica (Wilken, 1987; Barrera, 1988) are located in the first position of a hierarchical system that responds to the same logic of biological taxonomies (both in structure and in composition; Berlin, 1973). This important fact reveals that, within the farmers' indigenous classification, soils have the category of a 'life form', which means that the soil is viewed as a living entity.

Some of the data presented in this study supported this point of view. Thus we conclude that Mesoamerican knowledge about soils is at least four centuries more advanced than the current ideas about the relationships of soil organisms and soil fertility. Our results certainly suggest that in the remaining ancient knowledge of indigenous Mexican farmers, the soil and the animals inhabiting it are important factors indispensable to crop sustainability. This knowledge, unfortunately, was almost eliminated by Spanish conquerors.

Conclusions

Our findings suggest that indigenous farmers of Mexico, Peru and India consider earthworms as beneficial organisms for soil fertility. In the Congo, the small number of inquiries did not allow us to draw the conclusion that farmers do not care for these organisms. Moreover, in the Maalas system, women farmers could learn, once promoters explain this to them, how their traditional practice has favoured earthworms.

The general conclusion of this study is that, notwithstanding that some traditional knowledge exists, it is necessary to improve the education programme on soil biology, targeted at indigenous farmers. This programme should take into account the particular perceptions and beliefs in each region in order to adapt the new technologies. In this sense, development workers can build on the judgement, intuition, knowledge and experimental capacity of local people.

Development will then take place as a local adaptation of exogeneous technologies and knowledge, and enhance the diversity in lifestyle and biological resources. With increasing recognition of the value and the need for working with local communities to identify, test, evaluate and disseminate new low-input technologies, various approaches will emerge (Haverkort and Millar, 1994).

For the near future, we need a radical change in the traditional ways of thinking about rural development. Indigenous peasant knowledge is often not seen by outsiders as valuable and valid in itself. It is seen as something to be taken into acount when introducing new technologies and concepts of development, whereas the main goal should be to find the best combination of elements of the indigenous system and the external system.

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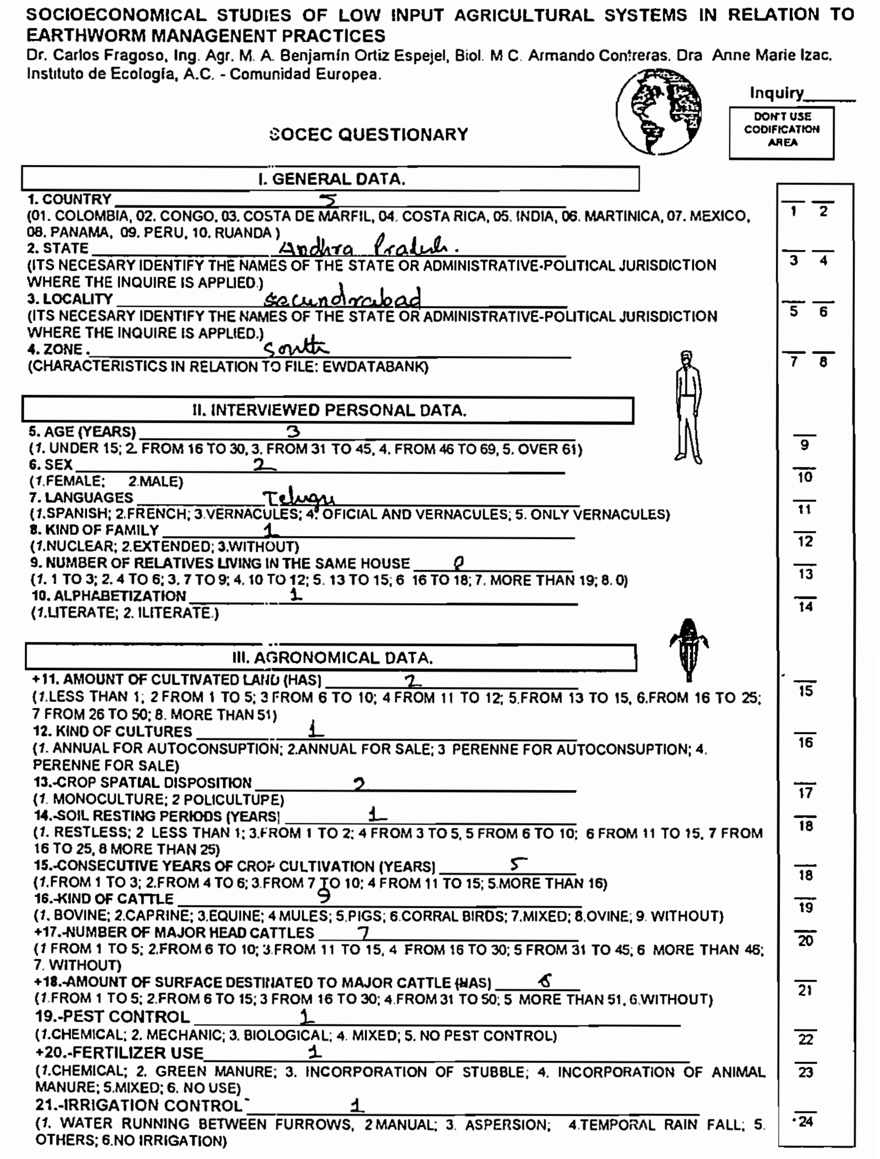
Appendix 8.1.



SOCIOECONOMICAL STUDIES OF LOW INPUT AGRICULTURAL SYSTEMS IN RELATION TO EARTHWORM MANAGENENT PRACTICES

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Instituto de Ecología, A.C. - Comunidad Europea.

Inquiry_____

DON'T USE CODIFICATION AREA

SOCEC QUESTIONARY

I. GENERAL DATA.

1. COUNTRY 5
(01. COLOMBIA, 02. CONGO, 03. COSTA DE MARFIL, 04. COSTA RICA, 05. INDIA, 06. MARTINICA, 07. MEXICO, 08. PANAMA, 09. PERU, 10. RUANDA)

2. STATE Andhra Pradesh.
(ITS NECESARY IDENTIFY THE NAMES OF THE STATE OR ADMINISTRATIVE-POLITICAL JURISDICTION WHERE THE INQUIRE IS APPLIED.)

3. LOCALITY secundrabad
(ITS NECESARY IDENTIFY THE NAMES OF THE STATE OR ADMINISTRATIVE-POLITICAL JURISDICTION WHERE THE INQUIRE IS APPLIED.)

4. ZONE . South
(CHARACTERISTICS IN RELATION TO FILE: EWDATABANK)

II. INTERVIEWED PERSONAL DATA.

5. AGE (YEARS) 3
(1. UNDER 15; 2. FROM 16 TO 30, 3. FROM 31 TO 45, 4. FROM 46 TO 69, 5. OVER 61)

6. SEX 2
(1.FEMALE; 2.MALE)

7. LANGUAGES Telugu
(1.SPANISH; 2.FRENCH; 3.VERNACULES; 4. OFICIAL AND VERNACULES; 5. ONLY VERNACULES)

8. KIND OF FAMILY 1
(1.NUCLEAR; 2.EXTENDED; 3.WITHOUT)

9. NUMBER OF RELATIVES LIVING IN THE SAME HOUSE 8
(1. 1 TO 3; 2. 4 TO 6; 3. 7 TO 9; 4. 10 TO 12; 5. 13 TO 15; 6 16 TO 18; 7. MORE THAN 19; 8. 0)

10. ALPHABETIZATION 1
(1.LITERATE; 2. ILITERATE.)

III. AGRONOMICAL DATA.

+11. AMOUNT OF CULTIVATED LAND (HAS) 2
(1.LESS THAN 1; 2 FROM 1 TO 5; 3 FROM 6 TO 10; 4 FROM 11 TO 12; 5.FROM 13 TO 15, 6.FROM 16 TO 25; 7 FROM 26 TO 50; 8. MORE THAN 51)

12. KIND OF CULTURES 1
(1. ANNUAL FOR AUTOCONSUPTION; 2.ANNUAL FOR SALE; 3 PERENNE FOR AUTOCONSUPTION; 4. PERENNE FOR SALE)

13.-CROP SPATIAL DISPOSITION 2
(1. MONOCULTURE; 2 POLICULTUPE)

14.-SOIL RESTING PERIODS (YEARS) 1
(1. RESTLESS; 2 LESS THAN 1; 3.FROM 1 TO 2; 4 FROM 3 TO 5, 5 FROM 6 TO 10; 6 FROM 11 TO 15, 7 FROM 16 TO 25, 8 MORE THAN 25)

15.-CONSECUTIVE YEARS OF CROP CULTIVATION (YEARS) 5
(1.FROM 1 TO 3; 2.FROM 4 TO 6; 3.FROM 7 TO 10; 4 FROM 11 TO 15; 5.MORE THAN 16)

16.-KIND OF CATTLE 9
(1. BOVINE; 2.CAPRINE; 3.EQUINE; 4 MULES; 5.PIGS; 6.CORRAL BIRDS; 7.MIXED; 8.OVINE; 9. WITHOUT)

+17.-NUMBER OF MAJOR HEAD CATTLES 7
(1 FROM 1 TO 5; 2.FROM 6 TO 10; 3.FROM 11 TO 15, 4 FROM 16 TO 30; 5 FROM 31 TO 45; 6 MORE THAN 46; 7. WITHOUT)

+18.-AMOUNT OF SURFACE DESTINATED TO MAJOR CATTLE (HAS) 6
(1.FROM 1 TO 5; 2.FROM 6 TO 15; 3 FROM 16 TO 30; 4.FROM 31 TO 50; 5 MORE THAN 51, 6.WITHOUT)

19.-PEST CONTROL 1
(1.CHEMICAL; 2. MECHANIC; 3. BIOLOGICAL; 4. MIXED; 5. NO PEST CONTROL)

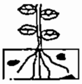
+20.-FERTILIZER USE 1
(1.CHEMICAL; 2. GREEN MANURE; 3. INCORPORATION OF STUBBLE; 4. INCORPORATION OF ANIMAL MANURE; 5.MIXED; 6. NO USE)

21.-IRRIGATION CONTROL 1
(1. WATER RUNNING BETWEEN FURROWS, 2 MANUAL; 3. ASPERSION; 4.TEMPORAL RAIN FALL; 5. OTHERS; 6.NO IRRIGATION)

Appendix 8.1. *Continued*

22.-KIND OF TILLAGE 2 25
(1 MANUAL; 2.WITH ANIMALS, 3 MECHANICAL; 4 MIXED)
23.-WEED CONTROL 1 26
(1.MANUAL; 2 MECHANICAL; 3.CHEMICAL; 4 MIXED; 5.NO CONTROL)
24.-UTILIZATION OF HARVEST REMANENT 2 27
(1 BURNED IN THE FIELD; 2 LEFT IN THE FIELD, 3 INCORPORATED TO SOIL, 4 USED LIKE FOOD CATTLE; 5 USED LIKE ENSILES; 6.MIXED)
25.-CROP ROTATION NO 28
(1 YES; 2 NO)
26.-YIELD OF PRINCIPAL CROP (KG/HA) 3 29
(1.FROM 1 TO 20; 2.FROM 21 TO 100; 3.FROM 101 TO 500; 4 FROM 501 TO 1000; 5 FROM 1001 TO 1500; 6 FROM 1501 TO 2000; 7. FROM 2001 TO 3000; 8. FROM 3001 TO 4000; 9. MORE THAN 4001)
27.-YIELD OF SECONDARY CROP (KG/HA) 2 30
(1.FROM 1 TO 20; 2.FROM 21 TO 100; 3.FROM 101 TO 500; 4 FROM 501 TO 1000; 5 FROM 1001 TO 1500; 6. FROM 1501 TO 2000; 7.FROM 2001 TO 3000; 8 FROM 3001 TO 4000; 9 MORE THAN 4001)

IV.-ETHNOEDAPHOLIGICAL AND ETHNOBIOLOGICAL SOIL DATA



◆28.- AMOUNT OF SOILS RECOGNIZED X 31
(1.1; 2 2; 3 FROM 3 TO 4; 4.FROM 5 TO 7; 5.FROM 8 TO 10; 6.FROM 11 TO 15; 7.FROM 16 TO 20; 8 FROM 21 TO 25; 9. ANY ONE)
◆29.-PRINCIPAL CRITERION OF SOIL CLASIFICATION 1 32
(1.COLOR; 2.TEXTURE; 3.STONY; 4.PROFUNDITY, 5.TOPOGRAPHY; 6 INFILTRATION DEPTH; 7.PRESENCE OF ANIMALS LIKE EARTHWORMS, ANTS, TERMITES, 8.ORGANIC MATTER;
9 DONT'N KNOW)
◆30.-PRINCIPAL CRITERION OF SOIL FERTILITY 3 X 4 33
(1.TEXTURE; 2.DEPTH; 3 ORGANIC MATTER, 4.PLANT INDICATORS; 5 OTHERS, 6 DONT'N KNOW)
By seeing the growth of the plant we can say the soil is good

31.-SOIL VERTEBRATE RECOGNIZED 5 34
(1.FROGS; 2 BADGERS; 3.RATS; 4.OTHERS, 5.ANY ONE)

32.-SOIL INVERTEBRATE RECOGNIZED 5 35
(1.EARTHWORMS; 2.ANTS; 3.TERMITES; 4.OTHERS, 5 ANY ONE)

◆33.- EARTHWORMS RECOGNIZED 6 36
(1 1; 2 2; 3 FROM 3 TO 4; 4 FROM 5 TO 6; 5 MORE THAN 6)

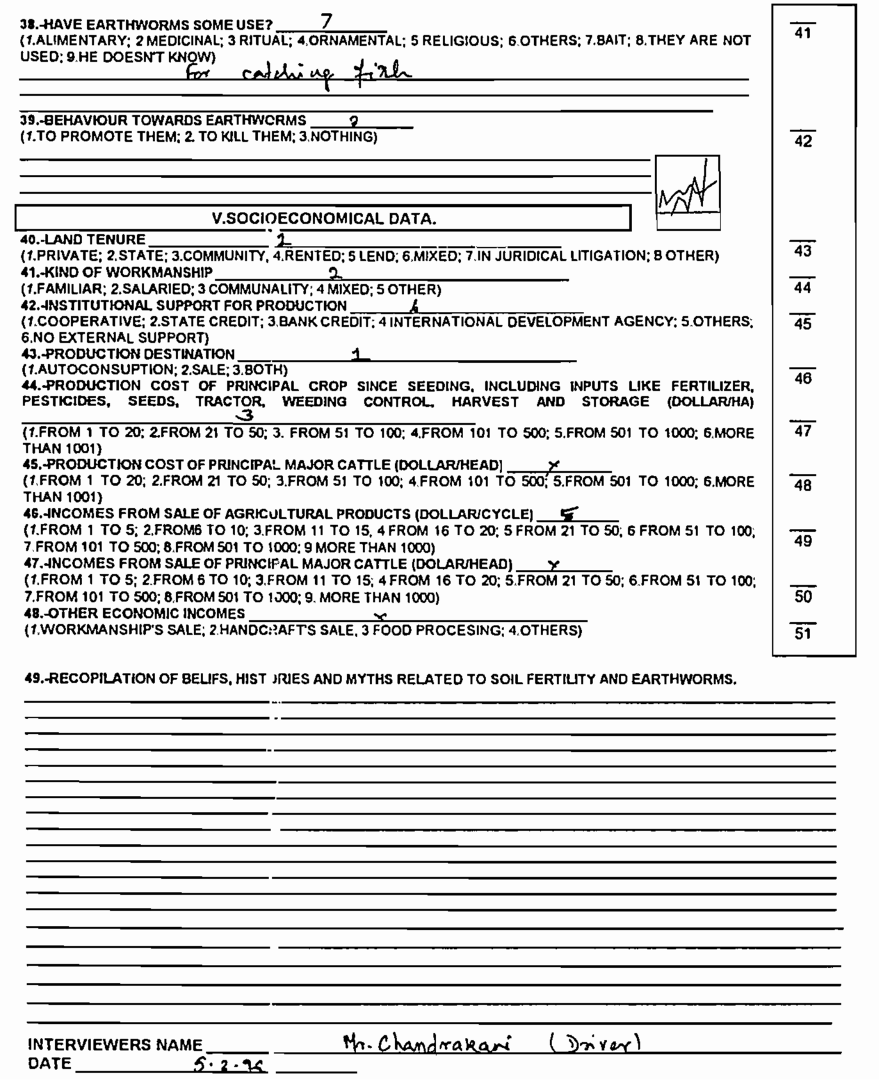
◆34.-PRINCIPAL CRITERION OF EARTHWORM IDENTIFICATION 1 & 2 37
(1.SIZE; 2 COLOR; 3 RESIDENCE PLACE; 4 LIFE CYCLE, 5 ASOCIATION TO NATURAL PHENOMENON; 6 OTHERS; 7. ANY ONE)

35.- EARTHWORM PREDATORS 2 & 3 38
(1.FROGS; 2.BIRDS; 3 SMALL MAMMALS, 4.OTHERS, 5.ANY ONE)

36.-ARE THE EARTHWORM BENEFICAL TO SOIL FERTILITY? 3 39
(1 YES, 2.NO; 3.HE (SHE) DOESN'T KNOW)

37.-ARE THE EARTHWORM HARMFUL TO SOIL FERTILITY? WHY? 3 40
(1.YES; 2.NO; 3.HE (SHE) DOESN'T KNOW)

Appendix 8.1 *Continued*



38.-HAVE EARTHWORMS SOME USE? 7 41
(1.ALIMENTARY; 2 MEDICINAL; 3 RITUAL; 4.ORNAMENTAL; 5 RELIGIOUS; 6.OTHERS; 7.BAIT; 8.THEY ARE NOT USED; 9.HE DOESN'T KNOW)
For catching fish

39.-BEHAVIOUR TOWARDS EARTHWORMS 2
(1.TO PROMOTE THEM; 2. TO KILL THEM; 3.NOTHING) 42

V.SOCIOECONOMICAL DATA.

40.-LAND TENURE 2
(1.PRIVATE; 2.STATE; 3.COMMUNITY, 4.RENTED; 5 LEND; 6.MIXED; 7.IN JURIDICAL LITIGATION; 8 OTHER) 43
41.-KIND OF WORKMANSHIP 2
(1.FAMILIAR; 2.SALARIED; 3 COMMUNALITY; 4 MIXED; 5 OTHER) 44
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INTERVIEWERS NAME Mr. Chandrakari (Driver)
DATE 5.2.95

Vermicomposting in the Tropics

9

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> Composting is perhaps the simplest example we have of man working in harmony with nature to keep its habitat in order and assure his own survival. The principle involved is nothing more than the first law of good house keeping, or good earthkeeping – when you are finished with something, put it back where it belongs.
>
> Steve Smmyser (Minnich and Hunt, 1979).

Summary

Different examples of vermicomposting technologies and programmes are briefly reviewed, focused primarily on tropical conditions. They offer options to multiply earthworms intensively and transform organic substrates for a wise utilization of natural resources, restoration or amelioration of ecological systems, contributing to create a better, sustainable agriculture.

With the aid of earthworms, waste materials are transformed into a material rich in nutrients readily available to plants, which can be added to agricultural land to improve soil structure and fertility, or as good quality and marketable additives to potting soil or plant growth media. They can be cultured systematically in a variety of designs and specific places under optimal environmental conditions, to accelerate the breakdown of different organic wastes. The case study of coffee pulp vermicomposting in Mexico shows how the development of this technology is suitable.

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Introduction

The widespread problems of soil degradation and desertification have emerged as important issues because they currently are threatening agricultural sustainability worldwide (Hanson and Cassman, 1994; Miller and Walli, 1994). Throughout the world, large human populations as well as industries and domestic animals increasingly are highly concentrated, producing locally large amounts of organic wastes and creating economic and environmental problems (*The Economist*, 1993).

These organic residues, byproducts or 'waste materials', if not used for other purposes, should be returned to the soil from which they were derived, thus ensuring the availability of adequate amounts of soil organic matter and nutrients.

With the aid of earthworms, waste materials can be transformed more quickly and into a more useful vermicompost, available for urban and farmland application. Nutrients within vermicomposted material are readily available to plants, and can be added to agricultural land to improve soil structure and fertility or used as a good quality and marketable additive to potting soil or plant growth media (Edwards and Bohlen, 1995).

History

As presented in detail by Bouché (1987), vermiculture has an interesting history, one which at times appears rather sordid because of illegitimate practices which were attributed to earthworm culturers and businesses.

In the 1970s, several publications and pamphlets mixed the roles of soil-dwelling earthworms from the field (endogeics and anecics) with those of the epigeics or compost earthworms in organic residue conversion. This mixture of true results and 'swindlings' gave rise to a presumed 'hybrid', 'domestic', 'Californian', exceptional 'earth-compost-earthworm', perfectly adapted to all requirements for intensive propagation and use and which obviously everyone should buy. Promoters presented very astute commercial arguments with great business expertise to farmers who were supposed to receive enormous earnings within a short time after buying this 'product'.

There was a rapid expansion in earthworm business in the United States during the 1970s (Carmody, 1996) and in Europe in the 1980s, due primarily to the popularity of residential 'buy-back' growing programmes. There were an estimated 100,000 people involved in these types of programmes in the late 1970s. Then in 1978, *The Wall Street Journal* (White, 1996) ran a major story, exposing the pyramid system that had invaded the booming earthworm growing business. By the spring of 1980, the boom had ended and the vermiculture industry, in spite of its promise of great things to come, declined. Almost overnight this fledgling industry disappeared. One clear message is that the earthworm business does *not* bring easy money, and culturers are advised to avoid mistakes or illegitimate practices such as those current in the 1970s.

However, there is scope for development of this technique in certain specific socioeconomic conditions. Furthermore, small-scale vermicomposting units for recycling household organic wastes are a very interesting proposition that could allow direct recycling of 30% of the weight of garbage produced in towns of developed countries (Anonymous, 1991).

Since 1978, the scientific communities and research programmes have given serious, critical, scientific analysis to vermiculture, re-establishing the effective potential tool that the compost earthworms represent. A body of knowledge has now been assembled on the possibilities offered by earthworms in organic waste management, their needs for breeding, their body composition, the quality of the organic matter obtained, and their effect on and potential uses in the soil, on plants and in general in the environment. There is now increasing scientific interest in assessing and developing the potential of processing large quantities of wastes using earthworms (Appelhof, 1981; Tomati and Grappelli, 1984; Edwards and Neuhauser, 1988).

Additionally, sessions on earthworms and waste management regularly have been included at the International Symposia on Earthworm Ecology (Satchell, 1983; Bonvicini-Pagliai and Omodeo, 1987; Kretzschmar, 1992; Hoerschelmann and Andres, 1994; Edwards, 1997, 1998).

In spite of the large body of scientific literature on vermiculture available from developed countries, little hard scientific work has been undertaken in tropical–developing country situations, where there is evidence of a huge potential for using earthworms to process organic wastes. The evidence for promoting vermiculture research in the developing world is:

1. The global environmental crisis has turned the attention of the developing countries to the poor, developing countries, facilitating the assessment and support of sustainable soil management practices.
2. As shown in a survey on waste and the environment made by Environmental Resources Ltd (*The Economist*, 1993), the solid waste composition in typical refuse from urban areas tends to have more organic materials in poor countries (60%) than those in middle-income (47%) and industrialized countries (25%; 30% in France; Anon., 1991).
3. Developing world countries throw away much of the available, often unused, plant or animal matter produced by agriculture and domesticated animals.
4. Soils in tropical regions are irreversibly degraded more easily than those of perhaps any other part of the inhabited world.
5. In poor countries, there exist major population pressures and risk factors associated with degradation of the natural resource base. At the same time, urbanization continues, individual consumption grows and the waste streams continue to be centralized.

6. Tropical countries have better and more uniform environmental conditions for vermiculture than those found in temperate countries.
7. There are lower labour costs and a greater labour supply.
8. Generally, lower amounts of metals, pesticides and contaminants are present in wastes.
9. Some well known compost earthworm species which might have a still unknown potential and application have never been bred or studied in certain tropical substrates.
10. The organic wastes of the cities are almost always disposed of on nearby open land, but are usually placed with all the other non-organic wastes into dumps, which are still referred to as 'landfills', as they become more complex and expensive to manage.

Breakdown of organic wastes by earthworms can turn such an overlooked and neglected asset into a profitable one and produce useful materials, at the same time minimizing environmental pollution. The culturing of earthworms can be used to process wasted organic matter in the tropics and make a valuable contribution to a major environmental problem.

Concept

The concept of vermicomposting started from the knowledge that certain species of earthworms grow and consume organic residues very rapidly, converting them into an earthlike, soil-building substance that forms a beneficial growing environment for plant roots. The earthworms that are involved in vermicomposting belong to the ecological category of epigeics (Bouché, 1977; Lavelle, 1981), which live in the litter and feed primarily on pure organic matter.

Vermicomposting could be defined as: the combination of biological processes, designs and techniques used systematically and intensively to culture large quantities of certain species of earthworms to speed up the stabilization of organic waste materials, which are eaten, ground and digested by the earthworms with the help of aerobic and some anaerobic microflora, and thereby naturally converted into much finer, humified, microbially active faecal material (castings), where important plant nutrients are held in a form much more soluble and available to plants than those in the parent compound.

The end-product, a decomposed faecal material (earthworm faeces or 'castings'), consists of very finely structured, uniform, stable and aggregated particles of humified organic material, with excellent porosity, aeration and water-holding capacity, rich in available nutrients, hormones, enzymes and microbial populations. Thus, this product is a valuable, marketable and superior plant growth medium.

Generally speaking, earthworm culture can perform at the same time, three major and useful functions:

- reduce the pollution potential of organic wastes;
- make good use of organic residues by their bioconversion into casts (a plant growth medium); and
- produce more earthworms to extend the vermicomposting areas, or as a high quality protein meal, suitable for inclusion in various domestic animal (e.g. livestock) rations.

In contrast with other traditional processes of composting, vermicomposting takes advantage of the biological and physiological capabilities of earthworms and their activities and qualities to enhance the aerobic microbial decomposition of organic materials.

The action of earthworms is performed in various ways (Sabine, 1983; Tomati *et al.*, 1987; Edwards and Bohlen, 1995):

1. While eating, they turn and maintain the substrate in an aerobic condition and cover the surface of the substrate with their faecal material or casts, reducing bad odours and numbers of unwanted animals such as flies.
2. They macerate the organic materials through their grinding gizzard, which strongly increases the exposed surface area and enhances the beneficial action of aerobic microorganisms. In fact, earthworms can derive part of their nourishment from the microorganisms that grow on the organic materials.
3. The beneficial microorganisms released from the earthworm gut continue their activity for some period outside the gut because of a favourable polysaccharide–mucoprotein medium produced, the 'peritrophic membrane', which impregnates each cast and retains many minute aggregates.
4. Different organic materials can be mixed together by earthworms, allowing an optimal combination and composition of the nutrient content, producing a much finer, fragmented and uniform material than by any other composting method.
5. There is considerable scientific evidence that plant and human pathogens do not survive the vermicomposting process, so if materials containing pathogens are used, they are, for the most part, killed in passing through the earthworm gut.
6. Small inorganic pieces, such as rocks, plastics or glass, hard to collect when mixed with the organics, are easily sieved after vermicomposting, due to the finer size of castings.
7. Contrary to common belief, earthworms do not have many serious natural enemies, diseases or predators.

Components of the System

To perform succesfully and produce an efficient and valuable plant growth medium, four principal components are needed for vermicomposting: (i) the proper substrates; (ii) the correct environmental conditions; (iii) appropriate earthworms with suitable population characteristics; and (iv) the designs and operations to be implemented.

Substrates

A wide range of organic materials for culturing earthworms are available in the tropics. These come from animal, vegetable, urban and industrial residues. Many of them are common or abundant in temperate climates (e.g. cattle, pig, horse, rabbit, sheep, turkey or poultry manures, anaerobically digested effluents, potato, brewery, paper pulp solids, olive residues, spent mushroom substrates, trimmings from floriculture industries, food scraps, grass clippings and other garden refuse, sawdust, urban and municipal solid wastes, etc.), but some others are found exclusively in tropical countries [e.g. coffee pulp, sugar cane and sisal-factory wastes, cocoa and coconut residues, water hyacinth and related water plants, banana stems, tropical wood scraps and sawdusts, cassava peel, tropical plant leaves, and Murrah Buffalo manure, among others (Table 9.1)].

The quality of the vermicompost produced from organic wastes depends very much on the original material that was used; it cannot be expected that a product with excellent fertilizing qualities will be obtained from inferior quality raw material. Table 9.2 lists the nutrient contents of a number of wastes processed by earthworms.

One of the most relevant characteristics of substrates supporting earthworm growth is the C/N ratio, which should be approximately 30/1. When different C and N ratios are present in organic wastes, then an appropriate mixture is recommended to attain this ratio.

Certain pesticides, heavy metals or other contaminants included in the raw materials can reduce the growth, reproduction and conversion rates of the earthworms (Hartenstein and Mitchell, 1978; Hartenstein *et al.*, 1980; Hartenstein, 1981; Ireland, 1983). Both the presence and high concentrations of these substances are found mainly in wastes produced in developed countries.

Detailed information on organic waste production (in particular, its quantity distribution, chemical content, problems created and actual uses) is scarce for most tropical countries. From this point of view, many organic materials still remain to be tested, with an unknown potential for vermiculture.

Environmental factors

One of the basic limiting factors to overcome in providing wastes for earthworms, is the heat generated during the initial decomposition of organic matter, the thermophilic process that can raise temperatures to more than 70°C; exposing earthworms to temperatures above 35°C will kill them.

Table 9.1. Average composition of some common natural organic materials.

	Composition (% by weight, dry basis)						
Organic material	N	P	K	Ca	Mg	S	Cl
Activated sewage sludge	6.0	1.0	—	1.8	0.9	0.4	0.5
Blood (dried)	13.0	—	—	0.4	—	—	0.6
Bone meal (raw)	3.5	19.8	—	22.5	0.6	0.2	0.2
Bone meal (steamed)	2.0	12.2	—	23.6	0.3	0.2	—
Castor pomace	6.0	0.6	0.4	0.4	0.3	—	0.3
Cocoa meal	4.0	0.6	2.1	0.4	0.6	—	—
Cocoa shell meal	2.5	0.4	2.5	1.1	0.3	—	—
Cocoa tankage	2.5	0.6	1.0	12.0	—	—	—
Cotton seed meal	6.6	1.1	1.2	0.4	0.9	0.2	—
Fish scraps (acidulated)	5.7	1.3	—	6.1	0.3	1.8	0.5
Fish scraps (dried)	9.5	2.6	—	6.1	0.3	0.2	1.5
Garbage tankage	9.5	0.6	0.8	3.2	0.3	0.4	1.3
Peanut meal	7.2	0.6	1.0	0.4	0.3	0.6	0.1
Peanut hull meal	1.2	0.2	0.7	—	—	—	—
Peat	2.7	—	—	0.7	0.3	1.0	1.1
Peruvian guano	13.0	5.5	2.1	7.9	0.6	1.4	1.9
Process tankage		8.2	—	—	0.4	—	0.4–
Soybean meal	7.0	0.5	1.3	0.4	0.3	0.2	—
Tankage (animal)	7.0	4.3	—	11.1	0.3	0.4	0.7
Tobacco stems	1.5	0.2	4.2	3.6	0.3	0.4	1.2
Whale guano	8.5	2.6	—	6.4	0.3	—	—

Manure source	Organic matter	N	P	K
Dairy	30	0.7	0.1	0.5
Goat	60	2.8	0.6	2.4
Horse	60	0.7	0.1	0.4
Pig	30	1.0	0.3	0.7
Poultry	50	1.6	0.5	0.8
Rabbit	50	2.0	0.6	1.0
Sheep	60	2.0	0.4	2.1
Steer	60	2.0	0.2	1.6

Source: Fairbridge and Finkl (1979) in Landon (1991).

Table 9.2. Major plant nutrient elements in worm-processed wastes.

	Element content (% dry weight)					
Waste material	N	P	K	Ca	Mg	Reference
Cattle solids (UK)	2.20	0.40	0.90	1.20	0.25	Edwards and Burrows (1988)
Cattle (Cuba)	1.70	0.62	1.22	10.0	1.53	Ramón and Romero (1993)
Cattle (Peru)	1.20	0.95	0.47	—	—	Ríos and Calle (1994)
Pig solids (UK)	2.60	1.70	1.40	3.40	0.55	Edwards and Burrows (1988)
Pig (Cuba)	1.89	0.50	0.34	10.8	1.46	Ramón and Romero (1993)
Sheep (Cuba)	1.51	0.64	0.78	4.40	1.37	Ramón and Romero (1993)
Sheep (Spain)	1.76	4.37	1.02	—	—	Albanell *et al.* (1988)
Sheep/cotton (Spain)	1.71	4.31	0.96	—	—	Albanell *et al.* (1988)
Sheep/orujo (Peru)	2.60	0.13	0.00	0.24	0.24	Quevedo (1994a)
Cattle (USA)	2.98	0.32	0.40	1.20	0.36	Fosgate and Babb (1972)
Cattle/straw (UK)	2.50	0.50	2.50	1.55	0.30	Edwards and Burrows (1988)
Pig/straw (UK)	3.00	1.60	2.40	4.00	0.60	Edwards and Burrows (1988)
Rabbit (Cuba)	1.23	0.28	0.67	—	—	Ramón (1992).
Duck/straw (UK)	2.60	2.90	1.70	9.50	1.00	Edwards and Burrows (1988)
Chicken/shavings (UK)	1.80	2.70	2.10	4.80	0.70	Edwards and Burrows (1988)
Leaves (Sweden)	0.8	0.34	0.82	1.96	0.53	Lofs-Holmin (1985)
Sugar cane (Cuba)	2.67	2.11	0.40	4.08	1.89	Ramón and Romero (1993)
Coffee pulp (Cuba)	2.01	0.27	2.14	1.96	0.37	Ramón and Romero (1993)
Coffee pulp (Mexico)	4.00	0.25	2.14	1.72	0.80	Irissón (1995)

Table 9.2. *Continued*

	Element content (% dry weight)					
Waste material	N	P	K	Ca	Mg	Reference
Coffee pulp (Colombia)	2.01	0.27	2.14	0.96	0.37	Dávila and Arango (1991)
Cassava peels (Nigeria)	1.98	0.14	1.80	0.40	0.14	Mba (1983)
Banana stems (Cuba)	2.50	0.56	3.74	2.36	1.50	Ramón and Romero (1993)
Rumin content (Cuba)	1.68	0.62	1.21	9.80	1.58	Ramón and Romero (1993)
Pharmaceutical residues (Italy)	3.10	0.82	0.26	8.80	0.54	Piccone *et al.* (1987)
Paper waste (Italy)	1.10	0.57	0.29	8.02	0.53	Piccone *et al.* (1987)
Food waste (Italy)	1.21	0.98	0.26	12.2	0.60	Piccone *et al.* (1987)
Food waste residues (Cuba)	0.90	0.44	3.60	3.60	3.10	Ramón and Romero (1993)
Commercial plant medium	1.80	0.21	0.48	0.94	2.20	Edwards and Burrows (1988)

Avoiding such overheating requires the addition of a relative narrow layer of organic material on the surface of the compost bed or heap, and allowing the earthworms to process the new residues under aerobic conditions; in this way, the earthworms will always be concentrated in the upper layer of waste.

Optimal conditions for breeding earthworms are provided for *Eisenia fetida* and *E. andrei* by Lofs-Holmin (1985) and Edwards and Neuhauser (1988), who suggested that these conditions do not differ much from those suitable for the other species (Table 9.3).

Earthworms

Although there are nearly 6500 described species of earthworms in the world (Fragoso, personal communication), only a few are known to be suitable for culturing in organic waste materials, and even fewer have been used on a widespread scale. Since only a few have been tested and many species are still to be discovered, it is likely that more species may become suitable candidates in the near future if research is continued.

Table 9.3. Optimal conditions for breeding *E. fetida* in animal and vegetable wastes.

Condition	Requirements
Temperature	15–20°C (limits 4–30°C)
Moisture content	80–90% (limits 60–90%)
Oxygen requirement	Aerobicity > 15% O_2
CO_2 content	< 6%
Redox potential	Eh > –100 mV
Ammonia content	Low: < 0.5 mg g^{-1}
Salt content	Low: < 0.5%
pH	> 5 and < 9

The best known species, with potential for waste management, include: *E. andrei* (red earthworm), *E. fetida* (brandling or tiger earthworm), *Eudrilus eugeniae* (African nightcrawler) and *Perionyx excavatus* (oriental compost earthworm). A few other species have been used under specific conditions (*Drawida nepalensis, Lampito mauritti, Dichogaster* spp., *Polypheretima elongata, Amynthas* spp., *Dendrobaena octaedra, Eisenia hortensis*) and they will not be discussed here.

Eisenia andrei *(Bouché, 1972) and* Eisenia fetida *(Savigny, 1826)*

The most commonly used earthworm species worldwide to process organic matter is *E. fetida*, the tiger or brandling worm, and the closely related *E. andrei*, the red worm, once both confused as *E. fetida*. Both have wide temperature tolerances and can live within a wide range of moisture contents; both are hardy earthworms, readily handled, and in mixed cultures (with other species) usually become dominant (Edwards and Bohlen, 1995).

Lumbricus rubellus (red worm) is believed to be suitable for organic waste breakdown, but this has yet to be substantiated. Surveys by Edwards in the USA and Europe and by Buckerfield and Baker in Australia showed that the species sold to commercial earthworm farms under the name *L. rubellus* were all *E. fetida* or *E. andrei* (Edwards, 1995).

Perionyx excavatus *(Perrier, 1872)*

This tropical earthworm is extremely prolific for use in vermiculture and is almost as easy to handle as *E. fetida* or *E. andrei* and very easy to harvest. It can be an ideal species for tropical conditions. It is a very common species in Asia and is used extensively in vermiculture in the Philippines and Australia (Edwards, 1995; Guerrero, 1983).

Eudrilus eugeniae *(Kinberg, 1867)*
Another suitable species is *E. eugeniae*, the African nightcrawler, which has received increased attention as a protein source and waste decomposer in tropical conditions, except that it appears to be less cold temperature tolerant and easily escapes during heavy rains (Graff, 1974; Rodríguez *et al.*, 1986; Neuhauser *et al.*, 1988; Edwards and Niederer, 1988).

Compared with other vermicomposting species, *E. eugeniae* seems to have a clear initial growth advantage as a potential protein producer (Viljoen and Reinecke, 1989). Some basic facts about the life cycle and reproduction of this species under favourable conditions are well documented in the literature (Viljoen and Reinecke, 1989; Rodríguez, 1996).

Design and Operation

Systems of growing earthworms range from very low technology, discontinous systems, such as windrows, heaps, pits, boxes, bins or containers stacked in racks, to more advanced continuous systems with applications from small-scale domestic to sophisticated, large capacity, completely automated vertical reactors. Each of them has its own specific advantages, and can be adapted to handle different volumes, environmental factors or economic conditions.

Discontinuous systems

The traditional method of vermiculture has been based on beds or windrows on the ground containing material up to 20–60 cm deep; the earthworms will always move upwards to follow the addition of successive thin layers of food on the surface of beds. Thicker layers only should be added if the material is mixed with the castings, to reduce the heat generated, which could kill the earthworms.

Generally speaking, the basic systems for growing earthworms, in terms of the position of the beds, are pits or heaps. Pits, under the surface soil level, have lower aeration but better water retention; on the other hand, heaps above soil level can have more lateral aeration, but lower water retention. It is usually easier to work with and construct a heap, but the choice has to be adapted to specific situations.

Horizontal windrows require large areas of land for large-scale production and are relatively labour intensive, but are the most common and widely used in the tropics. The relative low cost of human labour, low technology input, large availability of land and abundance of substrates make it the most feasible method.

All these methods also imply a discontinuous system, in which one needs to interrupt the vermicomposting process to separate most of the earthworms, to collect the end-product and to start again with a new successive series of food.

Continous systems

Much more satisfactory techniques have used containers raised on legs above the ground. These allow raw materials to be added at the top from mobile suppliers and the transformed end-product to be collected mechanically at the bottom through mesh floors using breaker bars. Such methods, first developed by engineers at the National Institute for Agricultural Engineering, in Silsoe, UK, range from relatively low technology instruments to completely automated driven reactors. These were operated successfully for more than 2 years using the original earthworm population and involving short retention times, fully processing up to 1 m deep layers of suitable organics in less than 30 days (Edwards, 1995).

An industrial-scale unit has been in place since 1991, as part of a total recycling system for a small town of La Voulte, on the Rhone river in south-eastern France. This plant can handle 30 Mg day^{-1} of mixed household waste. The organic material is separated with a rotating trommel and, after a thermophilic composting in agitated beds, the wastes are then vermicomposted in large, vertical bins called 'Lombricubateur' or 'Earthworm tanks' for around 60 days. These are housed in a climate-controlled room where proper temperature and humidity for optimum earthworm activity are maintained. It is estimated that a population of between 1 and 2 × 10^9 *E. andrei* and *P. excavatus* are required. At the end of the vermicomposting stage, the organic matter has been aggregated by earthworm gut transit and is easily sorted from other inorganic components not separated in the earlier process (Abdul and Abdul, 1994).

Based on similar principles, a small-scale system was designed and manufactured by an Australian commercial group and successfully sold for use in homes and domestic projects. The so-called 'Can-O-worm' consists of one bottom level for leaching and three working levels, each having hundreds of holes in the base to allow the earthworms to eat their way up to the next level. By the time the third working tray is put into place on top and filled with new organic materials, the bottom tray is ready for harvesting of the earthworm castings and is free of earthworms. It can then be placed on top, enticing the earthworms to move upward again, and the process continues indefinitely.

Quality and Nutrient Content of the Vermicompost

Depending on the parent material, the casts can be very rich in available nutrients, allowing not only an immediate supply of plant nutrients, but also build up of reserves for future crops. Casts have a superior bio-active potential, presenting plant growth hormones (Tomati *et al.*, 1983, 1987), suppressive effects on some root-infecting pathogens (Szczech *et al.*, 1993), enhanced levels of soil enzymes and high-soil microbial populations. Additionally, they are weed free and rich in humic compounds, creating an efficient and valuable soil-building medium (Table 9.2).

Some authors have examined the influence of chemical composition and mineralization of nitrogen to evaluate how vermicompost derived from differing organic wastes could be compared with other composts (Buchanan *et al.*, 1988). Others found that common chemical analyses and effects on growth revealed only minor differences between earthworm-worked wastes and those composted with conventional methods (Penninck and Verdonnck, 1987), so that vermicompost was considered superior to ordinary compost only due to its physical structure (Haimi and Huhta, 1987).

Vermicompost consists of a conglomeration of minute cylindrical aggregates formed by passage through the digestive canal of the earthworms; they contain very fine particles and a generally higher microorganism population than the parent raw material. All of them are covered by internal secretions of the earthworm and bacterial polysaccharides which cement organic particles together as they pass through the intestines of the earthworms (Van Gansen, 1962). The result is a very homogeneous, finely textured, odour free and visually appealing material, all decisive factors in increasing the chances of selling the medium for specialized agricultural use.

When the nutrient content is compared with that of a commercial plant growth medium to which inorganic nutrients have been added, earthworm castings (independently of their parent material) usually contain similar quantities of the main nutrients N, P, K, and most other mineral elements, supplying the bulk of the nutrient element needs of plants. Nevertheless, during the vermicomposting process, most of the nutrients are changed to forms more readily available to plants, e.g. nitrate, ammonium, exchangeable P and soluble K, Ca and Mg contained in the waste materials (Edwards and Bohlen, 1995).

Humic acids are a very important constituent of earthworm-worked material and are a natural by-product of the microbial decomposition or alteration of plant or animal residues and of cellular components and products synthesized by soil organisms. Some important and beneficial properties of humus are: slow release of plant nutrients, improvement of soil physical properties, enhancement of micronutrient element nutrition of plants through chelation reactions, help in the solubilization of plant nutrient elements from insoluble minerals, high adsorptive or exchange capacity for plant nutrient elements, increase in the soil buffer capacity, promotion of heat absorption and earlier spring planting (in cold climates), support of a greater and more diverse microbial population which favours biological control, including disease suppression, reductions of toxic chemical substances, both natural and man-made, and increased soil water-holding capacity (Martín and Focht, 1986).

There is also often a higher humic acid/fulvic acid ratio as well as a higher humification rate or humification index in many earthworm castings than in those materials obtained by other composting means. However, the results are not consistent in all materials, suggesting that it depends on the raw materials utilized (Casalicchio and Graziano, 1987).

Results of two seasons of work with earthworm-digested animal wastes used as a supplement with peat for hardy nursery stock grown in loamless compost in Efford Experimental Horticultural Station in the UK, suggest that the one major drawback to its wider use could be the variability of the product (e.g. soluble salts), not only between wastes of different animals, but also in wastes from the same source in different seasons (Scott, 1988).

Plant growth regulators, belonging to the auxin, giberellin and cytokinin groups present in the earthworm-worked materials, are produced by a wide range of soil microorganisms, many of which live in the guts of earthworms or within the castings (Grappelli *et al.*, 1983; Tomati *et al.*, 1983; Fontanesi, 1984).

Economic Evaluation

Sabine (1990) indicates that two major economic difficulties have faced current vermicomposting projects. First of all, they are expected to achieve financial viability as single, stand-alone operations, starting with, usually, just one type of waste. Secondly, generally no account is taken of the 'savings' made through replacement of alternative, non-productive disposal programmes. By contrast, he continues, 'waste-based agriculture' both charges a fee for the effective removal and disposal of biological waste and, more particularly, integrates vermicomposting into a much larger, integrated production system, utilizing a diverse range of biological starting materials and a range of both conventional and unconventional agricultural production systems.

More recently, new specific market niches have been developed, ranging from soil blenders and bulk consumers, to backyard gardeners; many companies in the US and other countries have demonstrated that different strategies are being used to grow a healthy business using earthworms. Vermicompost is now considered a type of 'gourmet' or luxury product that provides a real alternative to plant growth media and one of the best 'all-natural' soil-building substrates.

Manuals, Techniques and Scales in the Tropics

Despite the booming earthworm-growing business in the late 1970s in the US (there were an estimated 100,000 people mostly involved in residential 'buy-back' growing programmes), this movement did not spread to developing countries in the tropics, probably because at this time in these countries the intensive high-input agricultural systems were becoming stronger as a result of the commercial expansion of international equipment and agrochemical companies.

Only short, poorly documented and dispersed scientific reports from individuals and isolated activities on vermicomposting in developing tropical countries were available until recently, and these had always been overshadowed by the strong impulse of highly technological and conventional agriculture.

More recently, by the end of the 1980s, with the emergence of the internationally recognized concept of sustainable agriculture, vermicomposting and other soil management methods have become more accepted as a means of helping to reduce the problem of waste management.

In tropical developing countries, different efforts have been emerging on vermicomposting, beginning principally with the initial introduction of supposed 'Californian Hybrid' earthworms.

Although most of the technical information is based on literature from temperate countries, there are quite remarkable manuals from the tropics (Ramón *et al.*, 1989; Zarela *et al.*, 1993; Martínez, 1995, 1996). Most of the literature is from India (Beena and Sachin, 1993; Bhawalkar, 1993; Senapati, 1994) and from Latin America; Colombia (Dávila *et al.*, 1990; Arango and Dávila, 1991; Orozco *et al.*,1996), Chile (Velázquez *et al.*, 1986a,b; Venegas and Leticia, 1988; Azancot and Alvaro, 1989; López and Ricardo, 1989), Costa Rica (León *et al.*, 1992), Cuba (Ramón and Romero, 1993; Werner and Ramón, 1996), Ecuador (Barkdoll, 1994; Landín, 1994), Peru (Quevedo, 1994a,b) and Mexico (Aranda, 1988; Barois and Aranda, 1995; Irisson, 1995; Arellano, 1997).

This is not an exhaustive bibliographic query; certainly there is interesting work going on in other parts of Asia and Africa, but the information was not readily available for us.

Conclusions

Much work is yet needed to study and promote vermiculture in developing countries, because of the wide range of organic matter sources (plant and animal origin) available and mostly unused.

There is a clear lack of well documented information available from countries in the tropical developing world; thus the promotion of exchange, worldwide web information, experiences, research data and publications (at any level they are produced) would be a good start.

Correct identification of earthworms is essential in order to avoid the use of general terms such as 'Californian hybrid', 'red worm' and the not yet substantiated *L. rubellus*.

The source, distribution, amount and nutrient contents of potential organic sources produced in each country must be well assessed. Where this information is not yet available in a direct form, it could be deduced indirectly from agricultural or livestock production and related information.

The economic viability of the most common operations of vermicomposting units should be evaluated in order to determine the cost–benefit ratio, followed by an appropriate commercial market price for the finished product.

Vermicomposting of Coffee Pulp: a Case Study from Veracruz (Mexico)

Coffee pulp is the main by-product of the coffee industry and is produced when coffee beans are extracted from the fruit using the 'wet process'. Coffee pulp represents approximately 40% of the fresh fruit weight. The annual pulp production for the state of Veracruz is 120,163 Mg and for the whole country 536,910 Mg (Instituto Nacional de Estadística, Geografía e Informática, Gobierno del Estado de Veracruz, 1996). Mexico ranks sixth in the world for coffee production. The chemical characteristics (e.g. high acidity) of this by-product cause both water and soil pollution. In addition, where the pulp accumulates, its decomposition is self-inhibited owing to the phenomenon of natural silaging.

In 1988, *E. fetida* was reported on piles of coffee pulp in Veracruz, Mexico (Aranda, 1988), confirming its potential use for the production of compost, the reduction of waste and the elimination of contamination. In 1992, a scientific project was sponsored by the National Science and Technology Council (CONACyT) to study the transformation of the coffee pulp into organic fertilizer by earthworms (Barois and Aranda, 1995). Most of the objectives of this project were scientific, although it also turned into the stimulus for the promotion and development of vermicomposting in the coffee-producing regions of Mexico.

Macrofauna sampling in coffee pulp piles

Macrofauna were sampled in the upper 10 cm of two large piles of coffee pulp (20 × 20 × 5 m). At both sites, Diptera larva had the largest relative density (55–51%), followed by Oligochaeta 19% in one site and Acarina (35%) in the other. The other groups detected were Coleoptera, Thysanoptera and Collembola, among others (Fig. 9.1a). In terms of biomass, the most important group was Oligochaeta (75 and 89%), followed by Diptera (10–20%, Fig. 9.1b). Earthworm species found were *P. excavatus*, *Amynthas gracilis* and *Dichogaster* sp. These are the species that are most commonly found in coffee pulp piles. While searching for earthworm populations in different pulp piles in the Veracruz region, *E. fetida* was found in only a few cases.

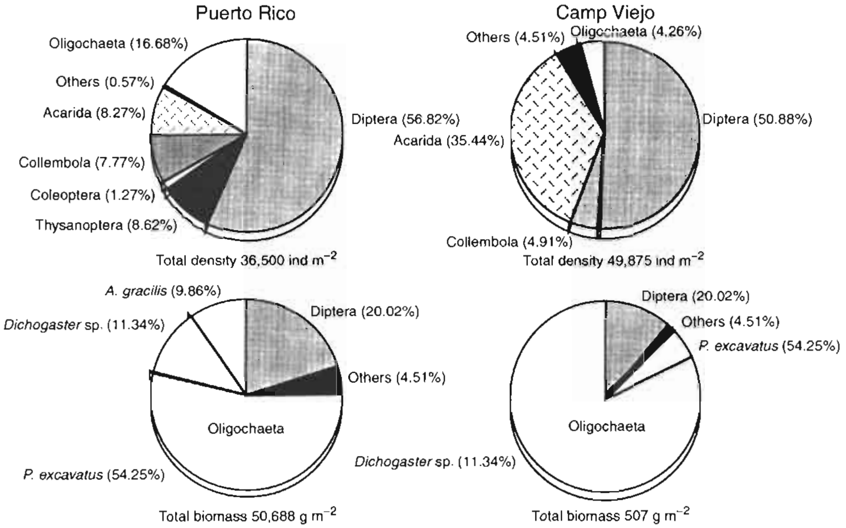

Fig. 9.1. Relative density and biomass of the invertebrate macrofauna from coffee pulp piles in Puerto Rico and Campo Viejo sites (Veracruz, Mexico).

E. andrei and *P. excavatus* development and the carrying capacity of coffee pulp under laboratory conditions

E. andrei and *P. excavatus* were reared separately in the laboratory in coffee pulp with population densities of two, four, eight, 16 and 32 individuals per box (15 × 15 × 5 cm), with four replicates per density class. Cow manure was used as a control for *E. andrei* and soil plus plant litter for *P. excavatus*, this being the substrate from which the latter species was collected (Arellano, 1997).

Both species performed fairly well in the coffee pulp. Individuals of both species grew more quickly in cow manure than in coffee pulp, reached sexual maturity sooner and exhibited a higher percentage of cocoon hatching and fertility. However, *E. andrei* produced more biomass and casts, and had lower mortality in coffee pulp than in cow manure, demonstrating the higher carrying capacity of coffee pulp (Table 9.4). On comparing the average maximum individual weight of *E. andrei* in different population densities, no significant differences were found ($P < 0.05$) among the different population densities or between the two substrates. However, the results for coffee pulp were more uniform than for cow manure (Fig. 9.2c and d).

P. excavatus did not exhibit good growth in the litter + soil substrate, probably because under laboratory conditions this resource became insufficient as a source of food and in terms of space. The maximum individual live weight for this species was significantly different ($P < 0.05$) between the two substrates tested (Fig. 9.2a and b). In coffee pulp, *P. excavatus* was two to three times

Table 9.4. Ecological and biological parameters of *P. excavatus* and *E. andrei* grown in coffee pulp substrate, in soil + litter and cow manure as their respective substrate controls (Arellano, 1997).

	Perionyx excavatus		*Eisenia andrei*	
	Coffee pulp	Soil + litter	Coffee pulp	Cow manure
Individual maximum weight	0.705 mg (b)	0.211 mg (c)	0.816 mg (a)	0.946 mg (a)
Theoretical maximum growth rate	80.58 mg earthworm^{-1} week^{-1}	19.07 mg earthworm^{-1} week^{-1}	60.22 mg earthworm^{-1} per week^{-1}	98.01 mg earthworm^{-1} week^{-1}
Substrate carrying capacity	532.44 g earthworm m^{-2}	74.22 g earthworm m^{-2}	3371.11 g earthworm m^{-2}	926.66 g earthworm m^{-2}
Appearance of clitellum	15–30 days	15–30 days	30–45 days	15–30 days
Average weight of mature individual	393 mg (b)	158 mg (c)	646 mg (a)	526 mg (a)
Cocoon distribution	Aggregated in coffee pulp fibres	—	Uniform throughout substrate	Uniform throughout substrate
Fecundity	Seven cocoons worm^{-1} week^{-1}	—	One cocoon worm^{-1} week^{-1}	Three cocoons worm^{-1} week^{-1}
Cocoon incubation	15–22 days	—	14–24 days	14–24 days
Cocoon hatched (%)	58%	—	85%	98%
No. of hatchlings	Two earthworms cocoon^{-1}	—	Three earthworms cocoon^{-1}	Three earthworms cocoon^{-1}
Fertility	Eight earthworms adult^{-1} week^{-1}	—	Three earthworms adult^{-1} week^{-1}	Nine earthworms adult^{-1} week^{-1}
Maximum estimation of cast production	5.4 g casts (a) g^{-1} earthworm day^{-1}	1.96 g casts (c) g^{-1} earthworm day^{-1}	3.72 g casts (a) g^{-1} earthworm day^{-1}	0.69 g casts (b) g^{-1} earthworm day^{-1}
Biomass production	15.59 mg biomass g^{-1} earthworm day^{-1}	9.09 mg biomass g^{-1} earthworm day^{-1}	28.18 mg biomass g^{-1} earthworm day^{-1}	14.59 mg biomass per g^{-1} earthworm day^{-1}
Mortality	2.4 %	18 %	4.4 %	33.4 %

Letters in parentheses within a row indicate significant differences ($P < 0.05$) based on multiple range test.

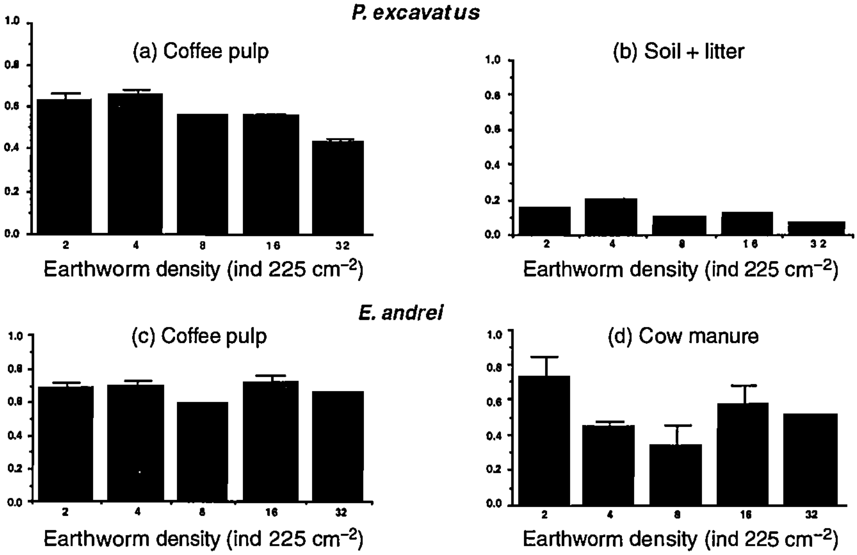

Fig. 9.2. Maximum individual weight of *P. excavatus* and *E. andrei* in different population densities and substrates (bars correspond to standard deviation).

heavier than in the soil + litter substrate. For both substrates, there was a significant difference ($P < 0.05$) in the maximum individual live weight of *P. excavatus* at different population densities. This species is more density dependent than *E. andrei*, and this is clearly evident from the differences in substrate-carrying capacity (maximum number or biomass of organisms that can be supported in a given area or habitat) 532.4 and 3371.1 g m^{-2}, respectively, for *P. excavatus* and *E. andrei* (Table 9.4).

In coffee pulp, *P. excavatus* individuals grew more rapidly, reached sexual maturity earlier and exhibited higher fecundity than *E. andrei*, while hatching rate and hatchlings per cocoons (fertility) was higher for *E. andrei* than for *P. excavatus*.

Cast production was more than five times its own live weight per day for *P. excavatus* and four times for *E. andrei*. In their respective control substrate, each species ingested less than 2 g daily.

P. excavatus presents an interesting prospect for vermicomposting in the field because it is more tolerant of temperature and pH variations and has higher capacity to invade the organic matter at earlier decomposition stages.

Comparative medium-scale vermicomposting of coffee pulp

This experiment was conducted with three species of earthworms: *P. excavatus*, *E. andrei* and *E. fetida*. Six wooden boxes measuring 1 × 1 × 0.4 m were placed outdoors and protected from rainfall. These were filled with an initial volume of

400 l of coffee pulp and inoculated with a starting population of 500 g of each earthworm species alone or mixed together. Two controls were used, one of mixed (overturning every 15 days) pulp and the other of untouched pulp. The overturned pulp was used because it reflects the treatment often used, although it is not economically viable because it requires considerable labour.

Temperature, pH, relative humidity and substrate volume were monitored before and after introducing the earthworms to the boxes. During the pre-inoculation period, the temperature reached a maximum of 32°C on the 7th day and this thermophilic phase ended on the 15th day when the boxes were inoculated with earthworms. At time 0 (when the pulp was put in the boxes), the pH of the coffee pulp was 4.1. pH became neutral on the 15th day (6.5–7.4) and then became basic (8–9) for 15 weeks. At the end of the decomposition process, the substrate in all the treatments was neutral and in the two controls was slightly acidic (Salazar *et al.*, 1995). During the process, there was a loss of 62% of the initial volume of the substrate. The evolution of the environmental parameters had similar tendencies in the different treatments, although the substrate was decomposed much more quickly when earthworms were present.

Organic fertilizer was produced in less than 150 days with earthworms present and in 200 days in the two controls (Fig. 9.3). At the end of the coffee pulp stabilization for the treatments with earthworms, the whole earthworm population was counted and weighed. Compared with initial biomass, final biomass tripled for *E. andrei* and almost tripled for *P. excavatus* and *E. fetida*. The treatment with the three species together reached the lowest biomass; however, this was still twice the inoculation biomass (Fig. 9.4a). The final

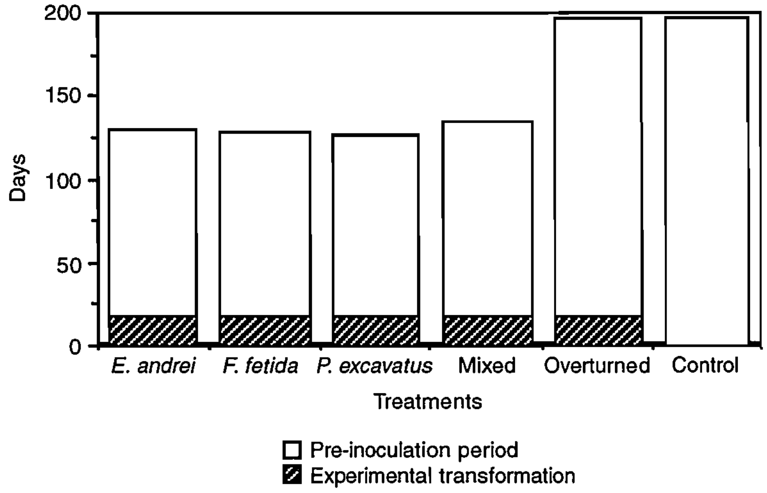

Fig. 9.3. Time elapsed for the transformation of coffee pulp into an organic fertilizer.

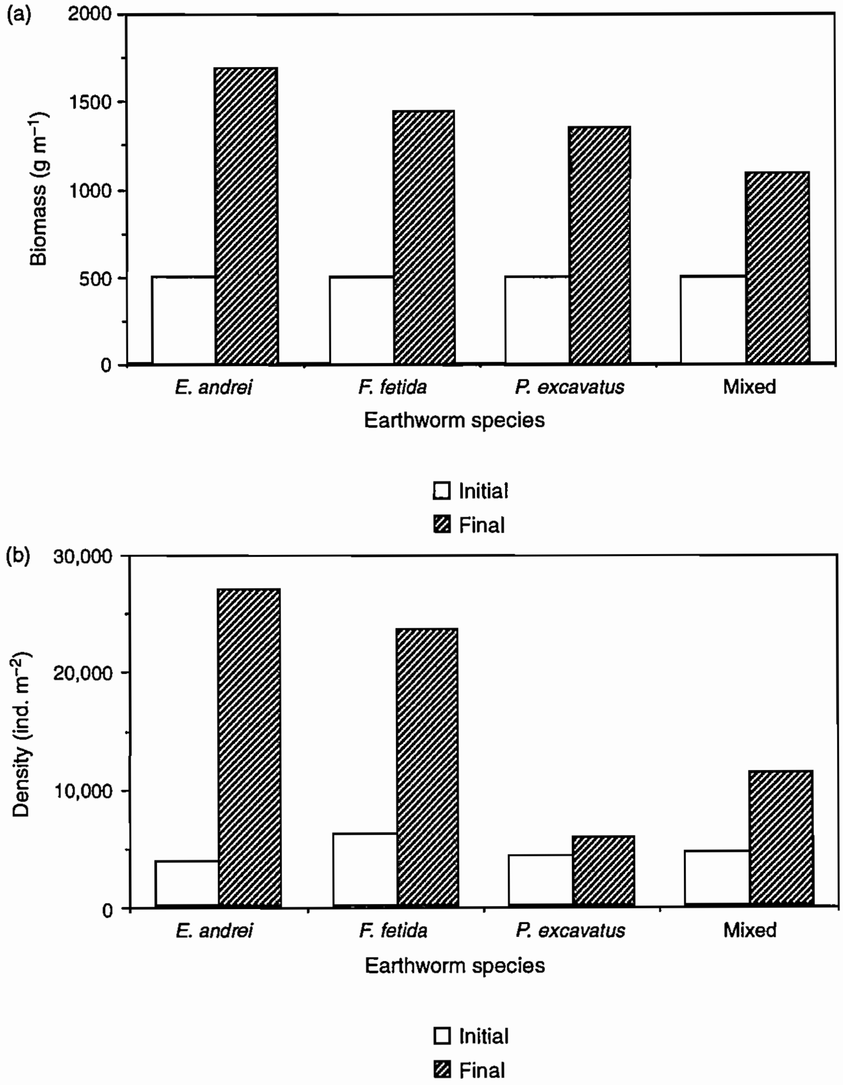

Fig. 9.4. Initial and final biomass (a) and density (b) of earthworms in 1 × 1 × 0.5 m containers.

density counts showed high density tolerance for *E. andrei* and *E. fetida*. The number of these species increased more than five times compared with the inoculated density. Apparently *Perionyx excavatus* did not even double its original number, but actually it demonstrated escaping behaviour (Fig. 9.4b). Thus, these data again indicate that *E. andrei* and *E. fetida* are better species for earthworm biomass production and more density tolerant. In addition, the results for the treatment with the three mixed species shows that a monospecific culture is more efficient for earthworm production than a polyspecific culture. The final biomass and density of *E. andrei* were 1.7 kg m^{-2} and 26,844 ind m^{-2}. Conversely, the mixed species treatment had a final biomass and density of 1.1 kg m^{-2} and 11,205 ind m^{-2} (elsewhere *E. andrei* became dominant).

Large-scale vermicomposting of coffee pulp

A simple design with full formed windrows (Fig 9.5) is being used successfully to vermicompost coffee pulp in open land in Coatepec, Veracruz since 1994. (Only 137,000 earthworms were inoculated on one bed of 2 × 50 m weeks after the thermophilic phase.) A periodic removal of the casts on both sides of the beds must be performed and combined with a manual blend, which permits the convenient mixing of the casts and earthworms with the immediately lower layers. When the whole substrate is nearly consumed, another interposed windrow is then formed, and the earthworms gradually move on their own to the new windrow on rainy nights.

So far more than 2500 trucks of 5 m^3 volume, filled with approximately 7500 Mg of coffee pulp from a large coffee factory have been transformed successfully with *E. andrei* and *P. excavatus*. This is the most recent large-scale experiment in the region (unpublished data). By the end of 1999, the sixth crop will be harvested. The casts produced have already been distributed in thousands of holes for new coffee plants in the fields.

Fig. 9.5. Windrows of vermicompost coffee pulp in open land in 'San Alfonso', Coatepec, Veracruz.

Table 9.5. Chemical characteristics of vermicompost obtained from coffee pulp (Iyissón, 1995).

	Treatments						
Analysis	CP	Ef	Ea	Pe	Mx	Ot	Ctrl
Water content (%)	**87.30**(a)	65.61(d)	64.66(e)	68.92(b)	60.64(g)	63.09(f)	66.99(c)
Total solid (%)	13.70(f)	34.39(d)	35.34(d)	31.08(e)	39.36(a)	**36.91**(b)	34.68(d)
pH	**7.08**(a)	6.51(c)	6.51(c)	6.72(b)	6.29(d)	6.02(e)	6.09(e)
Total nitrogen (%)	2.00(e)	**4.23**(a)	4.00(c)	4.07(b)	4.00(c)	3.30(d)	3.99(c)
N-NO_3 (p.p.m)	—	53.60(c)	1137.82(b)	1775.01(a)	1130.26(b)	**1806.57**(a)	18.45(c)
N-NH_4 (p.p.m)	—	538.54(e)	829.45(b)	**846.58**(a)	846.00(a)	652.85(d)	748.89(c)
Mineral nitrogen (%)	—	0.06(d)	0.20(b)	**0.26**(a)	0.20(b)	**0.25**(a)	0.08(c)
Organic nitrogen (%)	—	**4.17**(a)	3.80(c)	3.80(c)	3.80(c)	3.05(d)	3.91(b)
Total phosphorus (%)	0.11(g)	0.24(c)	0.25(b)	0.23(d)	0.22(d)	**0.26**(a)	0.20(f)
Inorganic phosphorus (%)	—	0.13(d)	0.14(bc)	0.14(bc)	0.15(b)	0.14(bc)	**0.19**(a)
Organic phosphorus (%)	—	0.11(a)	0.11(a)	0.09(b)	0.07(b)	**0.11**(a)	0.015(c)
Calcium (%)	0.75(e)	**1.73**(a)	**1.72**(a)	1.65(b)	1.50(d)	1.60(c)	1.40(d)
Magnesium (%)	0.36(g)	**0.82**(a)	0.80(b)	0.78(c)	0.69(f)	0.75(d)	0.73(d)
Sodium (%)	0.03(c)	**0.07**(a)	**0.07**(a)	**0.07**(a)	**0.07**(a)	**0.07**(a)	0.06(b)
Potassium (%)	0.35(e)	**0.78**(a)	0.73(b)	0.73(b)	0.70(c)	0.53(d)	0.52(d)
Copper (p.p.m.)	1.00(b)	**19.01**(a)	**19.68**(a)	**19.92**(a)	**19.79**(a)	**19.67**(a)	**19.93**(a)

Continued

Table 9.5. *Continued.*

	Treatments						
Analysis	CP	Ef	Ea	Pe	Mx	Ot	Ctrl
Iron (p.p.m.)	589.91(f)	2203.80(e)	5310.23(b)	4562.70(c)	4536.63(c)	**9250.73**(a)	3406.43(d)
Manganese (p.p.m.)	257.73(g)	643.32(e)	722.39(d)	745.52(c)	748.70(b)	**982.81**(a)	571.47(f)
Zinc (p.p.m.)	147.89(g)	**1287.76**(a)	662.55(e)	1103.63(b)	596.31(d)	886.46(c)	374.12(f)
Ash (%)	4.00(f)	12.70(e)	15.49(c)	17.29(b)	14.04(d)	**28.21**(a)	16.08(c)
Organic matter (%)	**96.00**(a)	87.30(b)	84.51(d)	82.71(e)	85.96(c)	71.79(f)	83.92(d)
Carbon (%)	**55.68**(a)	50.29(b)	48.84(c)	48.36(c)	49.86(b)	41.64(d)	48.68(c)
C/N ratio	**27.66**(a)	11.88(d)	12.22(c)	11.89(d)	12.47(bc)	12.62(b)	12.20(c)
Caffeine (%)	**0.022**(a)	0.007(d)	0.004(f)	0.006(e)	0.008(c)	0.008(c)	0.012(b)
Tannins (%)	**0.16**(a)	0.010(b)	0.010(b)	0.009(c)	0.012(b)	0.007(c)	0.014(b)
Lead	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Cadmium	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Strontium	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Organic compounds							
Humin (%)	—	84.22(a)	74.30(b)	70.34(c)	73.89(b)	83.95(a)	67.50(d)
Humic acids (%)	—	11.00(d)	15.11(b)	22.08(a)	13.76(c)	10.45(d)	22.68(a)
Fulvic acids (%)	—	4.78(d)	10.60(b)	7.58(c)	12.35(a)	5.60(d)	9.82(b)
Hum.ac/fulv.acid ratio	—	2.32(b)	1.43(d)	**2.93**(a)	1.11(d)	1.88(c)	2.32(b)

Enzyme assays							
Acid phosphatases IU g^{-1}	—	9.14(b)	**9.59**(a)	8.42(d)	6.99(f)	8.49(c)	7.83(e)
Alkaline phosphatases IU g^{-1}	—	**8.08**(a)	6.74(b)	5.71(c)	4.68(d)	3.88(e)	2.14(f)
Urease IU g^{-1}	—	**1.29**(a)	0.92(c)	1.08(b)	0.66(d)	0.17(f)	0.60(e)

CP, initial coffee pulp; Ctrl, stored coffee pulp; Ea, *Eisenia andrei*; Ef, *Eisenia fetida*; Mx, Three species together; Ot, overturning treatment; Pe, *Perionyx excavatus.*

Values in each row followed by the same letters are not significantly different ($P > 0.005$) using two-way ANOVA. n.d., not detectable

Table 9.6. Effect of the coffee pulp vermicompost or overturned compost and chemical fertilizers on coffee seedlings.

Treatments	Type of substrate	Type of fertilization	Plant height (cm)	Plant diameter (mm)	Dry aerial biomass (g)	Pair of leaves (n)	Dry foliar biomass (g)	Dry root biomass (g)	Root volume (ml)
1	S	WF	19.3 (abc)	5.0 (ab)	2.7 (bcd)	9.1 (abc)	2.0 (bcd)	1.1 (abcd)	5.7 (ab)
2		SF	14.2 (c)	3.6 (c)	2.4 (cd)	5.8 (c)	1.8 (cd)	0.6 (d)	2.7 (b)
3		FF	16.4 (c)	4.8 (ab)	1.9 (d)	8.2 (abc)	1.4 (d)	1.0 (bcd)	5.0 (ab)
4		BF	14.2 (c)	4.0 (bc)	2.4 (cd)	7.1 (bc)	1.9 (cd)	0.6 (cd)	3.2 (b)
5	S + PW	WF	25.5 (a)	6.0 (a)	5.6 (a)	12.3 (a)	4.3 (ab)	1.6 (ab)	7.1 (ab)
6		SF	21.2 (abc)	5.2 (ab)	4.3 (abcd)	10.9 (ab)	3.2 (abcd)	1.2 (abcd)	6.7 (ab)
7		FF	23.1 (ab)	5.6 (ab)	4.8 (abc)	11.5 (ab)	3.7 (abc)	1.2 (abcd)	6.1 (ab)
8		BF	23.2 (ab)	5.6 (ab)	4.6 (abcd)	10.8 (ab)	3.7 (abc)	1.3 (abc)	7.3 (ab)
9	S + PO	WF	23.7 (ab)	5.5 (ab)	5.8 (a)	11.4 (ab)	4.4 (a)	1.7 (a)	9.3 (a)
10		SF	20.7(abc)	5.0 (ab)	3.8 (abcd)	10.4 (ab)	2.9 (abcd)	1.3 (abc)	6.9 (ab)
11		FF	24.9 (a)	5.9 (a)	5.4 (ab)	12.7 (a)	3.9 (abc)	1.5 (ab)	6.9 (ab)
12		BF	22.7 (ab)	5.6 (ab)	4.2 (abcd)	10.1 (abc)	3.2 (abcd)	1.3 (abc)	6.8 (ab)

Substrate type: S, soil; S + PW, soil + coffee pulp vermicompost; S + PO, soil + coffee pulp overturned compost. Fertilization type: WF, without fertilizer; SF, soil fertilizer; FF, foliar fertilizer; BF, both fertilizers.

Values in each column followed by the same letters are not significantly different ($P > 0.05$) using a two-way ANOVA.

Chemical characteristics of coffee pulp vermicompost

At the end of the coffee pulp transformation under the six treatments previously mentioned, the resulting six composts and the initial coffee pulp were analysed. A homogenized sample with three replicates was used for each analysis.

The casting from coffee pulp had a well-balanced nutrient content (Table 9.5; Irissón, 1995), and a N content which is very high for a plant-derived compost (see Table 9.1). Earthworms appear to have stimulated ammonifying bacteria and depressed denitrifying ones in comparison with the overturned pulp treatment. In addition, enzyme activity in the vermicomposts was significantly higher ($P < 0.05$) than for the controls. The earthworms only mineralized approximately 10% of the carbon in coffee pulp compared with 25% in the overturned treatment. The harmful compounds, such as caffeine and tannins, are almost completely decomposed during the process in all six treatments, but were transformed the least in the control. The high percentage of humins in the vermicompost and overturned compost indicates a higher microbial activity than in the control. The total P content of the initial coffee pulp was low, although during decomposition it almost doubled, while the control had the lowest concentration. K content was low in all treatments, even in coffee pulp, because it was drained before collecting (see normal K content in Table 9.2).

The effect of coffee pulp vermicompost on coffee plant growth

An agronomic experiment was carried out with three different substrates: soil alone (S), 60% soil + 40% coffee pulp vermicompost (S + PW) and 60% soil + 40% overturned coffee pulp (S + PO). Four treatments of chemical fertilization were applied to each of these substrates: no fertilizer (WF), soil fertilizer (SF; NPK 18–12–06: 3 g applied twice per plant), foliar fertilizer (FF; 'Grow Green' NPK 20–30–10 plus micronutrients, 5 g l^{-1}, two applications) and both fertilizers (BF). A total of 280 plants were observed. Measurements of the plant parameters (Table 9.6; Rodríguez *et al.*, 1995) showed no significant differences between the plants grown on coffee pulp composted by earthworms and those grown on overturned pulp. Plants grown on soil alone differed significantly ($P < 0.05$) for most parameters. For example, plants grown on soil with coffee pulp compost were 44% taller than those grown on soil alone with the different fertilization regimes. Soil fertilization of the three substrates did not result in any positive effect, while foliar fertilization did produce a slight and similar positive effect on plants grown on all three substrates.

Currently, little scientific work is being done to test the effect of coffee pulp vermicompost although much empirical work is underway. Commercially, vermicompost is used as a growing substrate for coffee, tomato and other vegetables, such as broccoli, in 'normal' or 'high' agricultural technologies. Figures 9.6 and 9.7 show tomato and broccoli seedlings grown

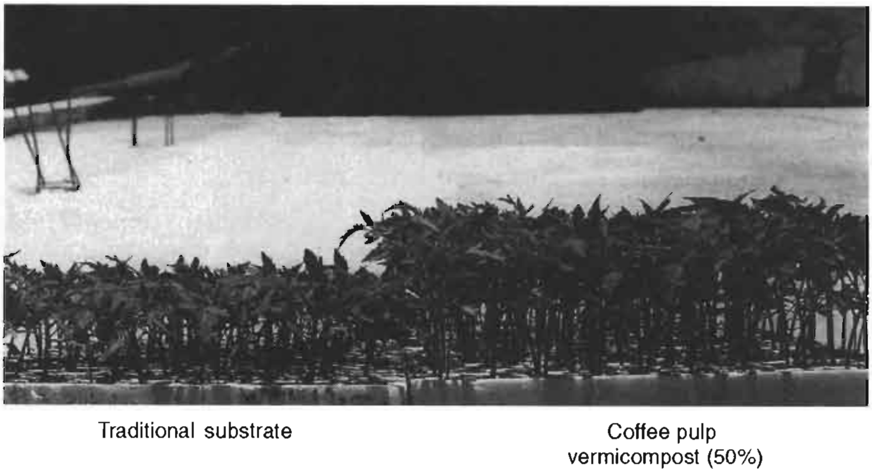

Fig. 9.6. Tomato (farmer technology) seedlings grown on traditional (peat moss-based) substrate and on coffee pulp vermicompost–peat moss (50 : 50 vol.).

Fig. 9.7. Broccoli (high technology) seedlings grown on traditional (peat moss-based) substrate and on coffee pulp vermicompost–peat moss (50 : 50 vol.).

on the traditional substrate and on coffee pulp vermicompost. These images speak for themselves! Figure 9.8 shows the greenhouses where the broccoli are grown on coffee pulp vermicompost + peat moss.

Vermiculture in the state of Veracruz

Since the above work was started at the Instituto de Ecología, many people have asked for information, and extension work has started. Over the course of 7 years, more than 20 large coffee producers and cooperatives have begun to work their pulp with earthworms, particularly with *E. andrei*, in windrows in open land or shaded under native or planted trees. Some keep the vermicompost for their own seedlings or sell it to plant growers. These days, coffee pulp is no longer considered a contaminating product and its value is starting to be recognized. Some vermicompost producers have started to make mixed substrates, combining vermicompost with volcanic dust or vermicomposted sugar cane residues.

This transition is occurring in other coffee-producing states as well. Furthermore, there is notable public demand for testing of vermiculture on other substrates, such as sugar cane residues, substrates used for growing mushrooms, paper industry residues and municipal residues, among others.

Fig. 9.8. Broccoli (high technology) seedlings grown in greenhouses on coffee pulp vermicompost–peat moss (50 : 50 vol.) in Queretaro State, Mexico).

Discussion and conclusions

Up to now, vermicomposting coffee pulp has provided a good solution for this residue. Coffee pulp is decomposed more rapidly than in the overturned pulp treatment. In the long run, it is a cheap process that results in two products, vermicompost and earthworms. The latter can be used as a protein source for animals (fish, pigs and poultry) or to increase vermicomposting capacities. Coffee pulp vermicompost is a high quality organic fertilizer and plant growth substrate.

It would be interesting to examine the organic matter fraction and microbiology of vermicompost more closely in order to study potentially useful biotic effects and phytohormones. One problem with this substrate is that its production is pulsed. The harvesting cycle of coffee crop is 5 months long, which means that the pulp must be stored and preserved in order to provide food for the earthworms during the following 7 months until the next crop is ready.

This substrate stops decomposing when it accumulates, and this previously was a problem. Now we can take advantage of this property to standardize the silaging process and thus maintain optimal quality of the vermicompost. Coffee pulp silage is being studied by Gaime-Perraud *et al.* (1991) and Gaime-Perraud (1995) as a part of a project funded by the European Union.

The success of the technology reported in this case study appears to be related to the purity of the residue, which is weed free, homogeneous and free from (or with a very low content of), contaminating substances, e.g. heavy metals, pesticides and, of course, important available plant nutrients.

In developing countries, there are still many agro-industrial and vegetal residues that are relatively uncontaminated and that are suitable for composting. These can be used to help solve health, environmental, agricultural and food problems at low costs. To achieve this, more work needs to be done to test new residues and determine their viability for processing with vermicomposting technology. The results of research carried out to date, along with the demand for the development of further applications, indicate that the value of this technology has only begun to be explored.

Acknowledgements

We thank Patrick Lavelle for his invitation to present this subject, George Brown for his corrections and comments on the manuscript, Bianca Delfosse for reviewing the English, and Carlos Fragoso for the earthworm identification. This research was partially funded by CONACyT-Mexico Project No. 045-N9108 and by the Instituto de Ecología, A.C., Soil Biology Project No. 902–08.

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Earthworm Management in Tropical Agroecosystems

Edited by P. Lavelle, Laboratoire d'Ecologie des Sols Tropicaux, ORSTOM, Bondy, France, L. Brussaard, Department of Environmental Sciences, Wageningen Agricultural University, The Netherlands, and P. Hendrix, Institute of Ecology, University of Georgia, Athens, USA

The considerable mechanical activities earthworms introduce into the soil have significant effects on microbial activities, organic resources and plant growth. In the longer term, they are also essential agents of soil conservation. This makes them a vital resource that should be identified and managed in any agroecosystem, particularly low input ones. There is great potential in their use to improve soil fertility and develop sustainable systems, particularly in the tropics, where soil degradation is widespread. Research into soil biological processes is increasingly seen as essential in addressing this problem.

This book covers all aspects of the ecology of tropical earthworm communities and their effects on soil properties and plant growth and examines the latest methods and technologies which facilitate their management for the maximum benefit to the farmer. It is written by leading experts in the field from Europe, South and Central America, Africa and Asia and is essential reading for soil biologists, agronomists and extension workers in tropical agriculture.

Cover illustration by Yvette Fabbri, UNESCO.

ISBN 0 85199 270 6

CABI *Publishing*

Wallingford, Oxon OX10 8DE, UK.
10 East 40th Street, Suite 3203, New York, NY 10016, USA.