

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 (\pm) 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 $+ 56.3\% \pm 9.3\%$ (SE) and $35.8 \pm 8.9\%$, 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.

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 below-ground) 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 m²) at Yurimaguas (Peru) to 50 m² 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 <i>et al.</i> (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 <i>et al.</i> (1996)
	Lamto, Ivory Coast	Savanna	1228	72.6	12.1	11.7	0.91	0.11	14.1	7.5	n.d	Derouard <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (unpublished data)
Ultisol	Mbalmayo, Cameroon	Secondary forest	1600	61.8	16.0	22.2	4	n.d.	n.d.	6.34	n.d.	Brussaard <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (unpublished data)
Eutric vertisol	St Anne, Martinique	New pasture	1580	25	15	60	1.4	0.14	10	6.25	37	Hartmann <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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	<i>P. maximum</i> 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	<i>P. maximum</i> 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)	<i>P. corethrurus</i>	3.5–22	Pashanasi <i>et al.</i> (1992), Ydrogo (1994)
	Tamil Nadu, India	120, 150 days	Tea	<i>P. corethrurus</i>	127	Giri (1995)
Buckets	Lamto, Ivory Coast	79, 84 days	Maize, <i>Panicum maximum</i>	<i>P. corethrurus</i> , <i>H. africanus</i> , <i>M. anomala</i> , <i>C. zielae</i> ,	12.5–128	Spain <i>et al.</i> (1992)
		69–74 days	Peanuts, rice maize	<i>S. porifera</i>	56.5	Derouard <i>et al.</i> (1997)
	Xalapa, Mexico	30 days–6 months	Beans, maize	<i>P. elongata</i> , <i>P. corethrurus</i>	32–63	Brown <i>et al.</i> (unpublished data)
	La Marquesa, Mexico	90 days	<i>Brachiaria decumbens</i>	<i>P. corethrurus</i>	114	Patrón (1998)
	Mbalmayo, Cameroon	65 days	Maize	At least two species	164	Brussaard <i>et al.</i> (unp. data)
PVC tubes	Sambalpur, India	~90 days	Rice	<i>D. willsi</i>	42.4	Senapati <i>et al.</i> (1985)
	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 Sambalpur	35–90 days 90 days	Maize Rice	<i>M. anomala</i> <i>D. willsi</i>	52 13	Gilot (1994, 1997) Senapati <i>et al.</i> (unpublished data)
	Narayan, Samford	14.5 months 13.2 months	<i>P. maximum</i> Various grasses	Nine species Ten species	8–166 7–166	Blakemore (1994)
	Curitiba, Brazil	9 months	<i>Mimosa scabrella</i>	<i>Amyntas</i> spp.	30–90	Kobiyama (1994)
Multi-crop field enclosures	Lamto Yurimaguas	3 years 3–7 years	Yam, maize Rice, cowpea, maize	<i>M. anomala</i> <i>P. corethrurus</i>	16–31.4 36	Gilot (1994) Pashanasi <i>et al.</i> (1994, 1996), Charpentier (1996)
	La Mancha, Mexico	3 years	Maize	<i>P. corethrurus</i> (<i>P. elongata</i>)	35.5	Patrón <i>et al.</i> (unpublished data)
Long-term field inoculation	Guarapuava, Brazil	1 year	Beans, wheat	<i>Amyntas</i> spp.	30–90	dos Santos (1995)
	Yurimaguas, Peru	3 years	Maize, cassava, cowpea, trees	<i>P. corethrurus</i>	1–36	Pashanasi <i>et al.</i> (unpublished data)
	Tamil Nadu, India	>3 years	Tea	<i>P. corethrurus</i> + four species	648	Giri (1995)
	St Anne, Martinique	>4 years	Pangola (<i>Digitaria decumbens</i>)	<i>P. elongata</i>	~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 m² 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	<i>n</i>	Overall % increase ^a	SE	<i>P</i> -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

^aValues with the same letters are not significantly different from each other at $P < 0.05$.

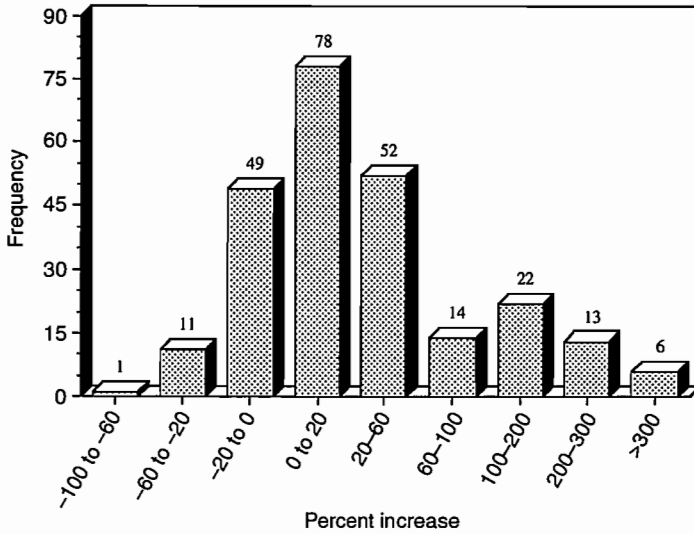


Fig. 4.1. Histogram of the frequency of increases in above-ground (shoot) plant biomass due to earthworms (the numbers above the bars indicate the number of cases). Data from the Macrofauna and other available experiments performed in the tropics (246 data points).

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 $\text{pH} < 5.6$, moderately acid soils $5.6 < \text{pH} < 7.0$ and alkaline soils $\text{pH} > 7.0$. 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 $\text{pH} < 5.6$ 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

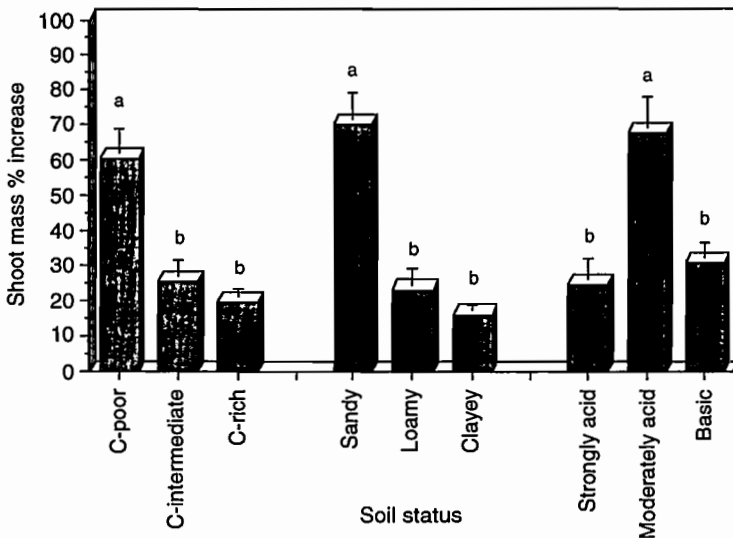


Fig. 4.2. Average percentage increase (+ SE bars) in above-ground (shoot) production due to earthworm activities in relation to soil texture, richness (%C), and pH, taken from a total of 221 data points. Poor soils had < 1.5% C, rich soils, > 3% C, and intermediate soils, 1.5 < %C < 3; sandy soils had > 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 $P < 0.05$.

Soil status	Plant part		
	Shoot	Grain	Root
	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.

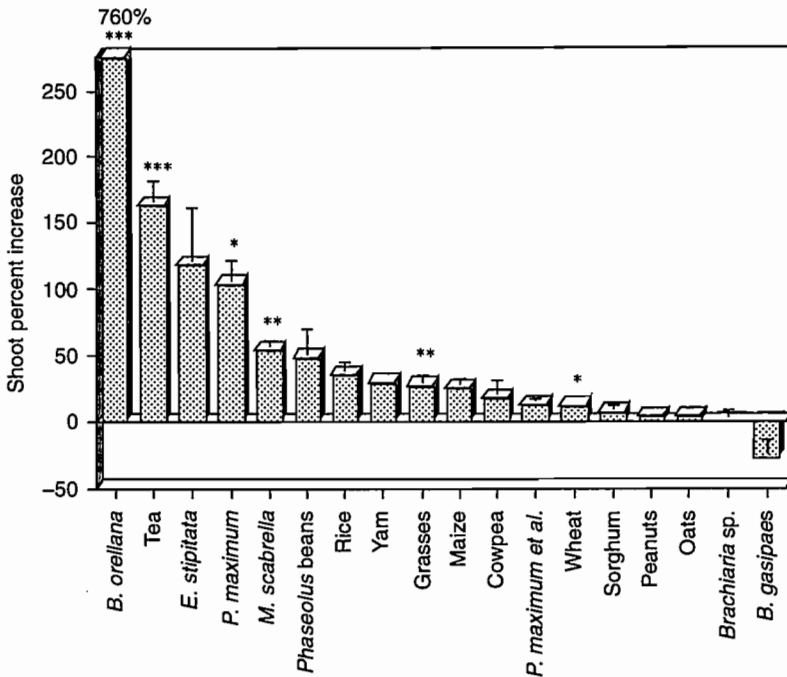


Fig. 4.3. Percentage increase (mean + SE bars) due to all earthworm species combined, of above-ground biomass of 17 plant species (from a total of 246 data points). Statistical significance of the *F*-test comparing the means of earthworm and non-inoculated treatments are shown as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. (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 4.2%, 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 graminaceous grain crops were always affected positively. Reasons for this may be different (generally higher) nutrient demands and root architecture, and the lack of symbiotic N₂-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. corethrus* + *Notoscolex* sp., *Metaphire* sp., *Megascolex* sp. and

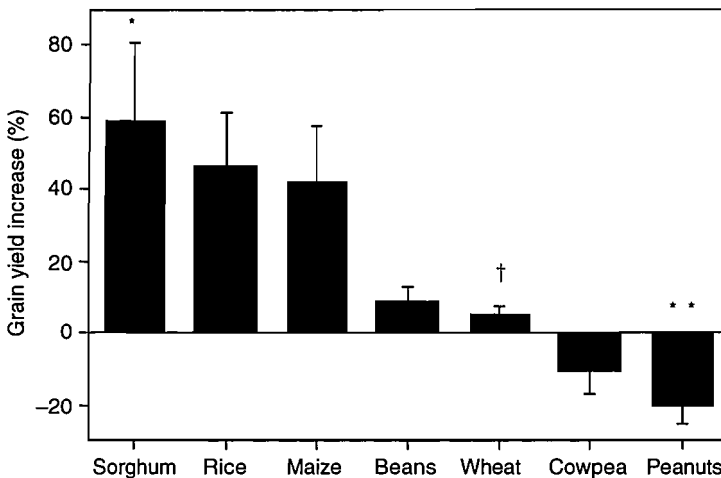


Fig. 4.4. Average percentage increase (+ SE bars) in grain biomass of seven annual crops due to earthworms (from a total of 89 data points). Statistical significance, when applicable, shown above the column ([†]*P* < 0.1); significance values as in Fig. 4.3.

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 results (see text)
<i>Pontoscolex corethrus</i> + others ^c	India	Tea	20	217.4	0.0001	-585.3	9.7	100	High ^d
<i>Pontoscolex corethrus</i> (mesohumic endogeic)	Peru, Mexico, India, Ivory Coast, Australia	Tea, trees, maize, rice	69	81.8	0.45	+22.6	323.4	65	High
<i>Chuniodrilus zielae</i> + <i>Stuhlmanina porifera</i> (polyhumic endogeics)	Ivory Coast	<i>Panicum</i> , maize	6	69.1	0.37	-5.6	123.3	100	High
<i>Drawida barwelli</i> + <i>Amyntas minimus</i>	Australia	Grasses	2	63.6	0.298	-23.9	0.32	100	Low
<i>Millsonia anomala</i> (mesohumic endogeic)	Ivory Coast	Maize, yam, <i>Panicum</i>	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	?
<i>Heteropordrilus bongeei</i>	Australia	Oats	1	39.6	-	-253.3	0	100	Low
<i>Polypheretima elongata</i> (mesohumic endogeic)	Mexico, Australia	Beans, sorghum	9	35.4	0.84	+19.1	126.7	50	Medium

<i>Aporrectodea trapezoides</i> + <i>Eisenia rosea</i>	Australia	Grasses	2	29.7	0.59	-164.0	1.2	100	Low
<i>Diploptrema</i> sp. nov. 1	Australia	Grasses, oats	9	25.1	0.49	-2.7	68.4	80	Medium
<i>Dichogaster</i> spp. (polyhumic endogeics)	Australia	Grasses	10	24.4	0.25	+46.5	321.4	70	High
<i>Drawida willsii</i> (epianecic)	India	Rice	6	23.8	0.71	+55.9	483.8	100	High
<i>Eisenia rosea</i> (mesohumic endogeic)	Australia	Oats	4	22.5	0.57	-134.8	1.2	75	Low
<i>Amyntas</i> spp. (polyhumic endogeics)	Australia, Brazil	Grasses, <i>Mimosa</i>	13	19.2	0.26	-18.4	68.4	84	Medium
<i>Millsonia anomala</i> + <i>Eudrilidae</i> ^e	Ivory Coast	Maize	3	13.5	0.70	-6.0	89.4	100	Medium
<i>Eudrilus eugeniae</i> (polyhumic endogeic)	Australia	Grasses	9	12.9	0.62	-77.3	35.5	66	Low
<i>Drawida barwelli</i>	Australia	Grasses	4	12.8	0.72	+4.8	113.7	75	Medium
<i>Polypheretima</i> <i>taprobanae</i> (mesohumic endogeic)	Australia	Grasses	5	11.2	0.64	-26.9	80.3	80	Medium
<i>Aporrectodea trapezoides</i> (mesohumic endogeic)	Australia	Sorghum, grasses	7	9.6	0.81	-48.4	93.4	100	Medium
<i>Hyperiodrilus africanus</i> (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)
<i>Pontoscolex corethrurus</i> + <i>Polypheretima elongata</i>	Mexico	Maize	12	5.9	0.89	?	n.d.	80	Low
<i>Fletcherodrilus unicus</i>	Australia		4	4.2	0.91	-140.6	23.2	75	Low
<i>Diploptrema</i> sp. nov. 2	Australia		2	3.6	0.94	+20.1	183.2	100	Medium
<i>Metaphire californica</i> (epigeic?)	Australia		4	3.2	0.98	-25.6	80	75	Medium
<i>Perionyx excavatus</i> (epigeic)	Australia		1	-1.2	-	-12.0	61.5	0	Low
<i>Eukerria saltensis</i> (polyhumic endogeic)	Australia		4	-2.4	0.89	+0.2	101.7	25	Low
<i>Octochaetus beatrix</i>	Australia	Oats	4	-3.5	0.84	-38.1	40.0	50	Low
<i>Ocnerodrilus occidentalis</i> + others ^f (polyhumic endogeics)	Australia		1	-11.6	-	-9.4	60.0	0	Low
<i>Digaster brunneus</i>	Australia		2	-12.2	0.81	-111.6	0	0	Low
<i>Spenceriella minor</i>	Australia		2	-22.5	0.60	-35.0	22.7	0	Low

^aCrops are mentioned only when increase is > 10%.

^bn = number of observations.

^cOther species added in low quantities were *Notoscolex* sp., *Metaphire houlleti*, *Megascolex konkanensis* and *Amyntas corticis*.

^dThis is a special case; see text for explanation.

^eOther species added were *C. zielae* and *S. porifera*.

^fOther species added were *Gordiogrillus elegans* and *Dichogaster bolau*.

Amyntas 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. corethrus*. 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 *Amyntas 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*, *Diploptrema* sp. nov. 1 and *Diploptrema* 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. corethrus* + 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), *Amyntas* spp. (109% of initial 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 adaptability) 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	<i>n</i>	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
<i>P. maximum</i> ^a	24	10.5	79	-0.9	50	—	—
<i>P. maximum</i>	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	—	—
<i>B. orellana</i>	5	760.7***	100	900.2***	100	—	—
<i>E. stipitata</i>	5	117.4	100	164.3	80	—	—
<i>B. gasipaes</i>	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 activities, 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 situation. 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

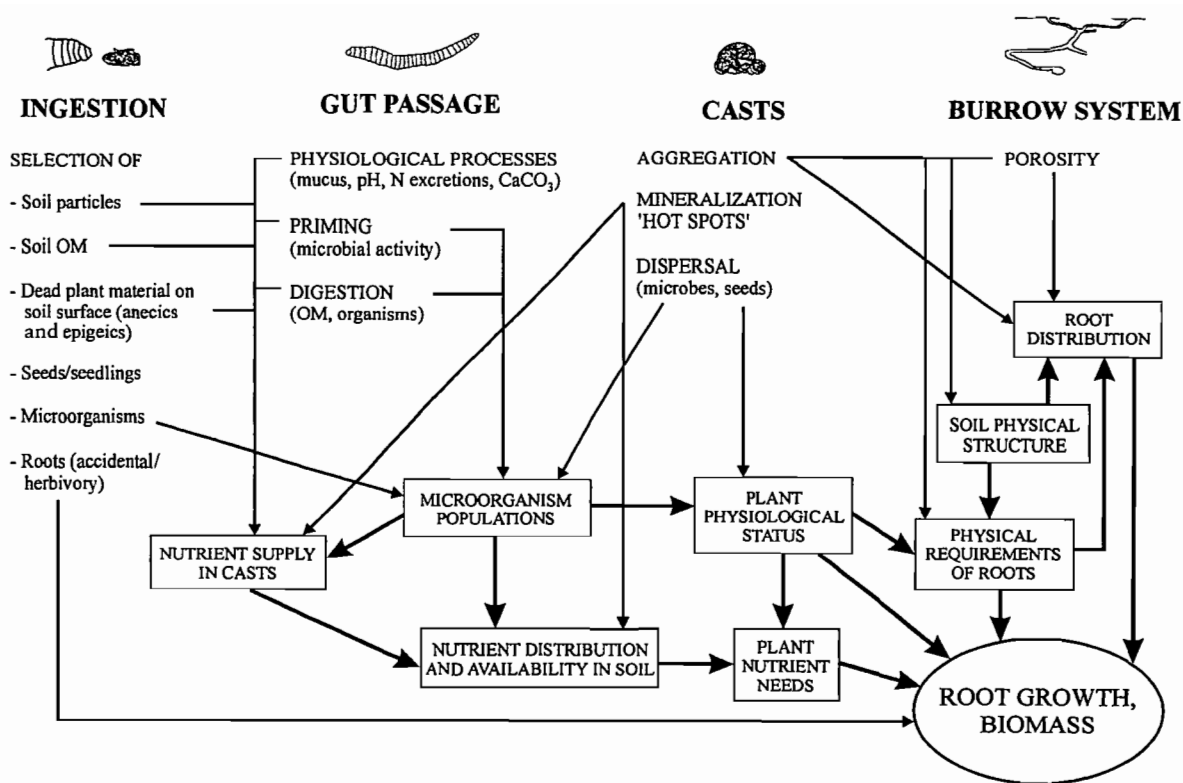


Fig. 4.5. Mechanisms by which the drilosphere properties (earthworm casts, burrows, gut) and its associated processes influence plant growth (especially roots).

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

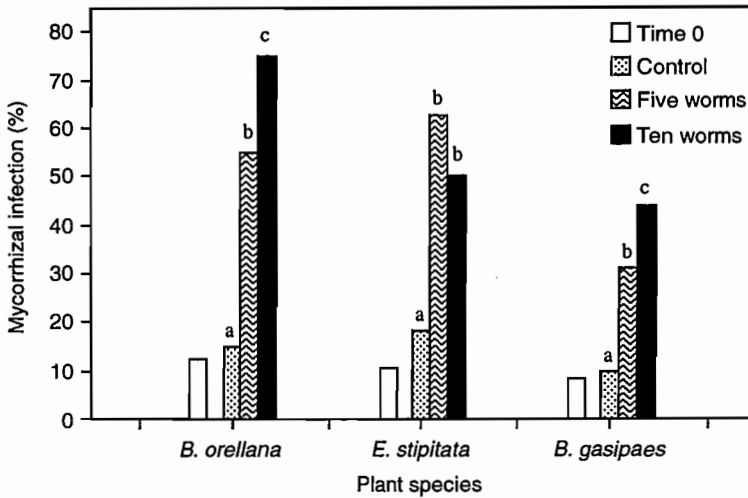


Fig. 4.6. Mycorrhizal infection in roots after various durations of greenhouse culture of tree seedling species *Bixa orellana* (120 days), *Eugenia stipitata* (240 days) and *Bactris gasipaes* (210 days) in the absence of earthworms (control), or in the presence of five (0.375 g) and ten (0.75 g) *P.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

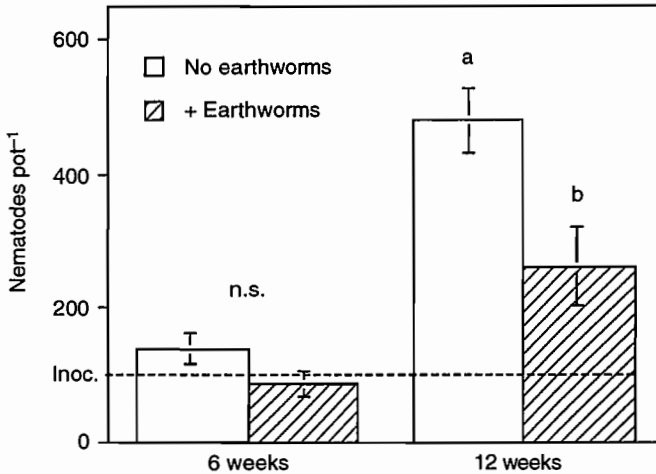


Fig. 4.7. Number of plant parasitic nematodes (*Pratylenchus zae*) recovered per pot after one and two generation times (6 and 12 weeks) in small pots planted with rice with and without *P. corethrurus* (Boyer, 1998). n.s. = differences not significant; different letters indicate significant differences 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 N₂ 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) N₂ 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; Pearce *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. corethrus* (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	<i>Aporrectodea rosea</i> , <i>A. chlorotica</i> , <i>Lumbricus terrestris</i>	Ferrière (1980)	
	<i>Nicodrilus caliginosus</i> , <i>Eisenia nordenskioldi</i>	Striganova (1982, 1984)	
	<i>L. rubellus</i> , <i>A. caliginosa</i> , <i>A. chlorotica</i> , <i>Aporrectodea longa</i>	(Pearce, 1978)	
	<i>P. corethrurus</i>	Reddell and Spain (1991a)	
	<i>Millsonia lamtoiana</i> , <i>Dichogaster terrae-nigrae</i>	Ka Kayondo (1984)	
	<i>Digaster</i> sp., <i>Heteropodrilus</i> spp.	Blakemore (1994)	
	<i>Anteoides</i> sp.	Németh (1981)	
	<i>Diplocardia longiseta</i> , <i>D. smithii</i> , <i>D. rugosa</i> , <i>D. prosenderis</i> , <i>D. verrucosa</i> , <i>A. turgida</i> , <i>Octalasion cyaneum</i>	James and Cunningham (1988)	
	Absent	<i>Dendrobaena mammalis</i> , <i>Lumbricus castaneus</i>	Pearce (1978)
		<i>L. castaneus</i> , <i>Nicodrilus longus ripicola</i> , <i>N. longus longus</i> , <i>N. caliginosus</i> , <i>A. icterica</i> , <i>N. nocturnus</i> , <i>D. mammalis</i>	Ferrière (1980)
		<i>Aporrectodea rosea</i>	Judas (1992), Bouché and Kretzschmar (1974)
		<i>M. anomala</i>	Lavelle (1971)
Several tropical species		Lavelle (1978, personal observation)	
<i>Andiorrhinus amazonius</i> , <i>Andiorrhinus</i> 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

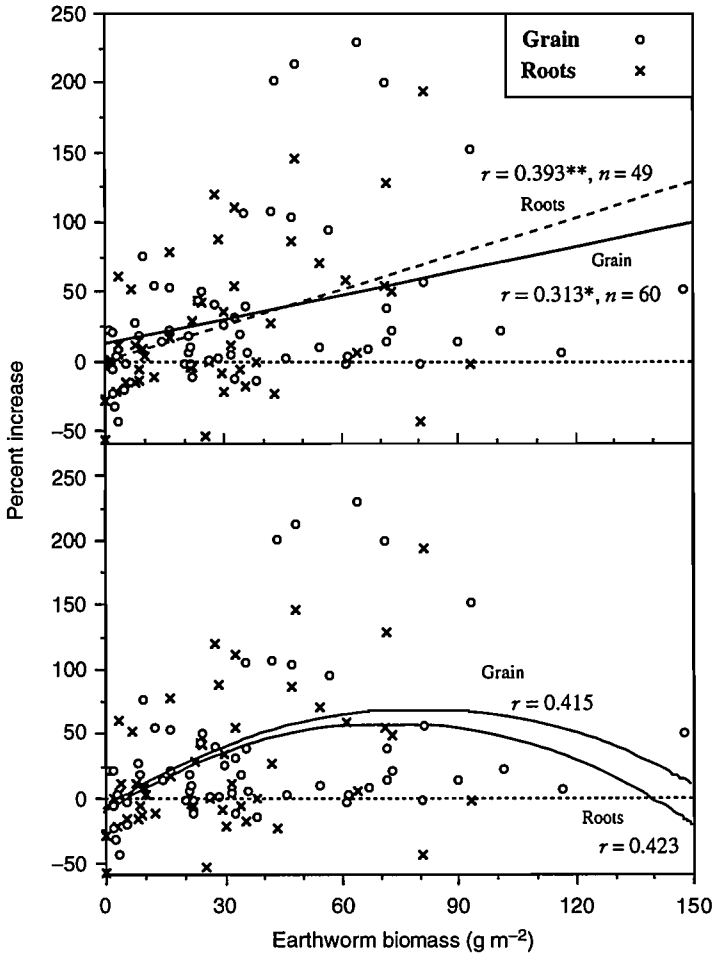


Fig. 4.8. Relationship between the increase in grain and root biomass due to the presence of earthworms and the difference in the biomass of earthworms obtained between worm addition and no-worm treatments for 60 (grain) and 49 (root) data points taken from 12 trials with six crops (maize, rice, sorghum, 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 $> 10,000 \text{ m}^{-2}$ (assuming average weights of $\sim 0.3 \text{ g worm}^{-1}$, 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, radish, 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 \pm SE of percentage increases of different plant parts (shoot, root, grain), due to the presence of earthworms in field trials and pot experiments.

Plant part	Field trials				Pot experiments			
	<i>n</i>	% Increase ^a	SE	<i>P</i> value ^b	<i>n</i>	% Increase	SE	<i>P</i> 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

^aValues with the same letters are not significantly different at $P < 0.05$; ^bResults 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.*,

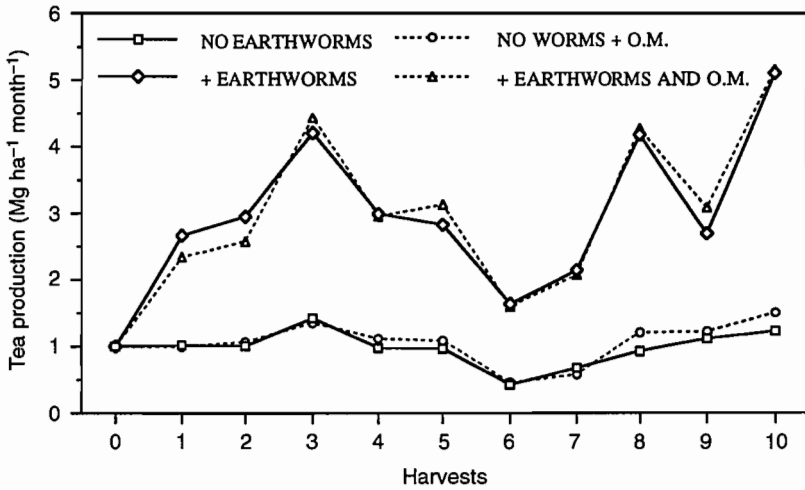


Fig. 4.9. Monthly green leaf tea production (in Mg ha⁻¹) as affected by the introduction of earthworms (primarily *P. corethrus*) and organic matter into trenches of 0.54 m² at Lower Sheikamuldi Tea Estate, Parry Agro Industries Ltd, Tamil Nadu, India (Giri, 1995; Senapati *et al.*, unpublished data).

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. corethrus* 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 (Narayan) 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 Narayan 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 *Amyntas* 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} ($\sim 90 g m^{-2}$) 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

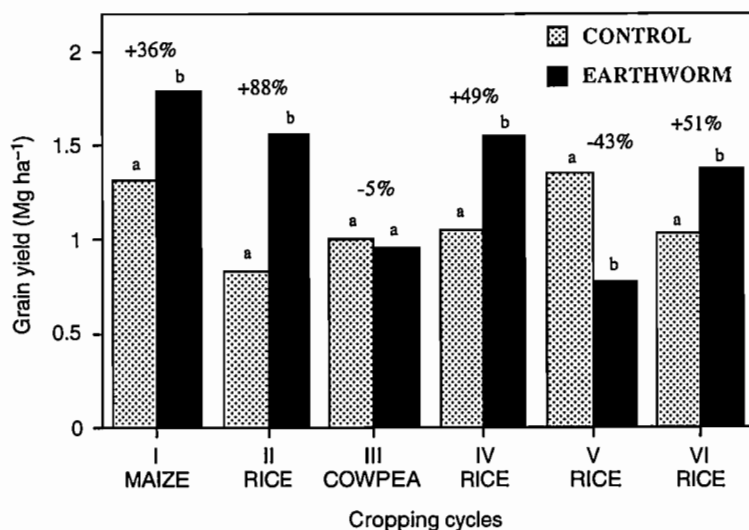


Fig. 4.10. Effect of earthworm (*P. corethrus*) activities on grain production (in Mg ha⁻¹) in field plots of 0.28 m² during six successive harvests over a 3-year period, irrespective of organic treatments, at Yurimaguas, Peru (Pashanasi *et al.*, 1994, 1996). Bars with different letters indicate significant differences at $P < 0.05$.

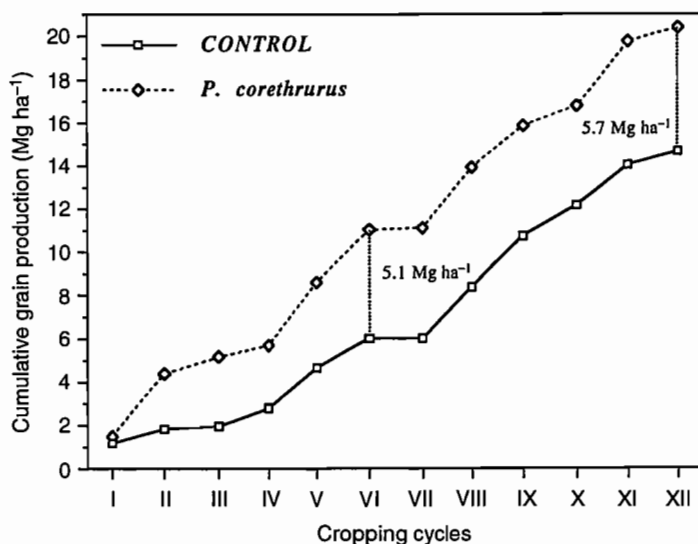


Fig. 4.11. Cumulative grain production of maize (in Mg ha⁻¹) over 7 years, including 12 cycles, in treatments with and without addition of 36 g m⁻² of *P. corethrus* at Yurimaguas, Peru (Charpentier, 1996; Pashanasi *et al.*, unpublished data).

of earthworms on production was positive in nine of the 12 cycles, and importantly so ($> 1 \text{ Mg ha}^{-1}$ 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 *Amyntas* 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 treatments 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 $> 1 \text{ m}^{-2}$, 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.

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References

- Amaravadi, L., Bisesi, M.S. and Bozarth, R.F. (1990) Vermial virucidal activity: implications for management of pathogenic biological wastes on land. *Biological Wastes* 34, 349–358.
- Barois, I. and Lavelle, P. (1986) Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biology and Biochemistry* 18, 539–541.
- Barois, I., Verdier, B., Kaiser, P., Mariotti, A., Rangel, P. and Lavelle, P. (1987) Influence of the tropical earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on the fixation and mineralization of nitrogen. In: Bonvicini Pagliai, A.M. and Omodeo, P. (eds) *On Earthworms*. Mucchi Editore, Modena, Italy, pp. 151–158.
- Barrion, A.T. and Litsinger, J.A. (1996) *Dichogaster nr curgensis* Michaelson (Annelida: Octochaetidae): an earthworm pest of terraced rice in the Philippine cordilleras. *Crop Protection* 16, 89–93.
- Barros, M.E., Blanchart, E., Neves, A., Desjardins, T., Chauvel, A., Sarrazin, M. and Lavelle, P. (1996) Relação entre a macrofauna e a agregação do solo em três sistemas na Amazônia central. In: *Solo-Suelo 1996, Proceedings of the XIII Latin American Congress on Soil Science*. Águas de Lindóia, Brasil. Software Gráfico Comércio e Serviços Ltda and Bicca Produções S/C Ltda, Campinas.
- Baylis, J.P., Cherrett, J.M. and Ford, J.B. (1986) A survey of the invertebrates feeding on living clover roots (*Trifolium repens* L.) using ^{32}P as a radiotracer. *Pedobiologia* 29, 201–208.
- Bhat, J. V., Khambata, S.R., Bhat, M.G., Sastry, C.A., Iyer, R.V. and Iyer, V. (1960) Effect of earthworms on the microflora of soil. *Indian Journal of Agricultural Science* 30, 106–114.
- Bhatnagar, T. (1975) Lombriciens et humification: un aspect nouveau de l'incorporation microbienne d'azote induite par les vers de terre. In: Kilbertus, G., Reisinger, O., Mourey A. and da Fonseca, J.A.C. (eds) *Humification et Biodégradation*. Pierron, Sarreguemines, France, pp. 169–182.
- Blakemore, R.J. (1994) Earthworms of Southeast Queensland and their Agronomic Potential in Brigalow Soils. PhD Thesis, University of Queensland, Brisbane, Australia.
- Blakemore, R.J. (1997) Earthworms of southeast Queensland and their agronomic importance in brigalow soils. *Soil Biology and Biochemistry* 29, 603–608.
- Blakemore, R.J. and Temple-Smith, M. (1995) Impact of earthworms on plant production. In: Temple-Smith, M. and Pinkard, T. (eds) *The Role of Earthworms in Agriculture and Land Management*. Technical Report 1/96, Department of Primary Industry and Fisheries, Tasmania, pp. 83–89.
- Blanchart, E. (1997) Rôle des systèmes biologiques dans le fonctionnement des vertisols (Martinique): application aux processus de restauration des propriétés physiques des sols. Final Report, SOFT Project, IRD, Fort-de-France, Martinique.
- Blanchart, E., Lavelle, P. and Spain, A. (1989) Effects of two species of tropical earthworms (Oligochaeta: Eudrilidae) on the size distribution of aggregates in an african soil. *Revue d'Ecologie et Biologie du Sol* 26, 417–425.
- Blanchart, E., Lavelle, P. and Spain, A. (1990) Effect of biomass and size of *Millsonia anomala* (Oligochaeta: Acanthodrilidae) on particle size aggregation in a tropical

- soil in the presence of *Panicum maximum* (Graminae). *Biology and Fertility of Soils* 10, 133–120.
- Bouché, M.B. and Kretzschmar, A. (1974) Fonctions des lombriciens II. Recherches méthodologiques pour l'analyse qualitative de la matière organique végétale ingérée (étude du peuplement de la station R.C.P.-165/P.B.I). *Revue d'Ecologie et Biologie du Sol* 11, 127–139.
- Boyer, J. (1998) Interactions Biologiques (Faune, Ravageur, Parasites, Microflore) dans des Sols sous Cultures en Milieu Tropical Humide (Ile de la Réunion). PhD Thesis, University of Paris VI.
- Brossard, M., Lavelle, P. and Laurent, J. Y. (1996) Digestion of a vertisol by an endogeic earthworm (*Polypheretima elongata*, Megascolecidae) increases soil phosphate extractability. *European Journal of Soil Biology* 32, 107–111.
- Brown, G.G. (1995) How do earthworms affect microfloral and faunal community diversity? *Plant and Soil* 170, 209–231.
- Brown, G.G. (1999) Confirmation of earthworm activity in plant rhizospheres using stable isotopes. *Rapid Communications in Mass Spectrometry*, in press.
- Brown, G.G., Bueno, J., Barois, I., Hernández-Castellanos, B., Frago, C. and Lavelle, P. (1998) Seasonal dynamics of the earthworm community and its interaction with soil properties and pasture production in a native paddock at La Vibora, Mexico. In: *6th International Symposium on Earthworm Ecology, Vigo, Spain, 31 August–4 September, 1998*. Abstracts, p.176.
- Carpenter, A. (1985) Studies on Invertebrates in a Grassland Soil with Particular Reference to Root Herbivores. PhD Thesis, University of Wales, Bangor, UK.
- Chapuis, L. (1994) Les Transformations du Phosphore d'un sol ferrallitique par un Ver Géophage, *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). MSc Thesis, University of Nancy I, Nancy. 54 pp.
- Chapuis, L. and Brossard, M. (1995) Modifications et stabilité du phosphore échangeable d'un ferralsol ingéré par un ver géophage. *Comptes Rendus de l'Académie de Sciences de Paris, serie IIa* 320, 587–592.
- Charpentier, F. (1996) Effet de l'Inoculation du Ver de Terre *Pontoscolex corethrurus* sur la Dynamique de la Matière Organique dans une Culture Continue de Maïs en Amazonie Péruvienne. PhD Thesis, Université de Paris VI. 161 pp.
- Cortez, J. and Bouché, M.B. (1992) Do earthworms eat living roots? *Soil Biology and Biochemistry* 24, 913–915.
- Dalby, P.R., Baker, G.H. and Smith, S.E. (1996) 'Filter paper method' to remove soil from earthworm intestines and to standardise the water content of earthworm tissue. *Soil Biology and Biochemistry* 28, 685–687.
- Darwin, C. (1881) *The Formation of Vegetable Mould Through the Action of Worms with Observations on their Habits*. Murray, London. 153 pp.
- Derouard, L., Lavelle, P., Tondoh, J. and Vilcosqui, L. (1996) Species specific effects in the response of tropical annual crops to the inoculation of earthworms: short-scale experiments at Lamto (Côte d'Ivoire). *Soil Biology and Biochemistry* 29, 541–545.
- dos Santos, A.F. (1995) Efeito da Atividade do Oligochaeta *Amyntas* spp. (Minhoca Louca), na Produção do Feijoeiro (*Phaseolus vulgaris* – FT 120) e da Aveia Preta (*Avena strigosa* var Canton), com Relação a Algumas Propriedades físicas, Químicas e Biológicas do Solo. MSc Thesis, Universidade Federal do Paraná, Curitiba. 72 pp.
- Doube, B.M. and Brown, G.G. (1998) Life in a complex community: functional interactions between earthworms, organic matter, microorganisms, and plants.

- In: Edwards, C.A. (ed.) *Earthworm Ecology*. St Lucie Press, Boca Raton, Florida, pp. 179–211.
- Doube, B.M., Ryder, M.H., Davoren, C.W. and Stephens, P.M. (1994a) Enhanced root nodulation of subterranean clover (*Trifolium subterraneum*) by *Rhizobium trifolii* in the presence of the earthworm *Aporrectodea trapezoides*. *Biology and Fertility of Soils* 18, 169–174.
- Doube, B.M., Stephens, P.M., Davoren, C.W. and Ryder, M.H. (1994b) Earthworms and the introduction and management of beneficial soil microorganisms. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. and Grace, P.R. (eds) *Soil Biota: Management in Sustainable Farming Systems*. CSIRO, East Melbourne, pp. 32–41.
- Ferrière, G. (1980) Fonctions des lombriciens VII. Une méthode d'analyse de la matière organique végétale ingérée. *Pedobiologia* 20, 263–273.
- Galli, E., Tomati, U., Grappelli, A. and Di Lena, G. (1990) Effect of earthworm casts on protein synthesis in *Agaricus bisporus*. *Biology and Fertility of Soils* 9, 290–291.
- Gilot, C. (1994) Effets de l'Introduction du Ver Géophage Tropical *Millsonia anomala* Omodeo en Système Cultivés sur les Caractéristiques des Sols et la Production Végétale en moyenne Côte d'Ivoire. PhD Thesis, Institut National Agronomique Paris-Grignon, France. 178 pp.
- Gilot, C. (1997) Effects of a tropical geophagous earthworm, *Millsonia anomala* (Megascolecidae), on soil characteristics and production of a yam crop in Ivory Coast. *Soil Biology and Biochemistry* 29, 353–359.
- Gilot, C., Lavelle, P. and Ganry, F. (1996) Effects of a tropical geophagous earthworm, *Millsonia anomala*, on some soil characteristics, on maize-residue decomposition and on maize production in Ivory Coast. *Applied Soil Ecology* 4, 201–211.
- Giri, S. (1995) Short Term Input Operational Experiment in Tea Garden with Application of Organic Matter and Earthworm. MPhil Thesis, Sambalpur University, India. 254 pp.
- Grant, J.D. (1983) The activities of earthworms and the fates of seeds. In: Satchell, J.E. (ed.) *Earthworm Ecology: From Darwin to Vermiculture*. Chapman and Hall, New York, pp. 107–122.
- Hand, P. and Hayes, W.A. (1983) Significant interactions between the earthworm *Eisenia fetida* (Savigny) and the microflora of cow slurry. In: Tomati, U. and Grappelli, A. (eds) *Proceedings of the International Symposium on Agricultural and Environmental Prospects in Earthworm Farming*. Tipolitografia Euromodena, Modena, Italy, pp. 177–182.
- Hamoui, V (1991) Life-cycle and growth of *Pontoscolex corethrurus* (Müller, 1857) (Oligochaeta, Glossoscolecidae) in the laboratory. *Revue d'Ecologie et Biologie du Sol* 28, 469–478.
- Hartmann, C., Blanchart, E., Albrecht, A., Bonneton, A., Parfait, F., Mahieu, M., Gaullier, C. and Ndandou, J.F. (1998) Nouvelles techniques de préparation des vertisols en culture maraîchère à la Martinique: Incidence pédologiques et socio-économiques. *Agriculture et Développement* 18, 81–89.
- Hopp, H. (1954) The facts about earthworms. In: *Let an Earthworm be Your Garbage Man*. A report by Home, Farm and Garden Research Inc.
- James, S. and Cunningham, M.R. (1988) Feeding ecology of some earthworms in Kansas tallgrass prairie. *American Midland Naturalist* 121, 78–83.
- Judas, M. (1992) Gut content analysis of earthworms (Lumbricidae) in a beechwood. *Soil Biology and Biochemistry* 24, 1413–1417.

- Kale, R.D., Bano, K., Secilia, J. and Bagyaraj, D.J. (1989) Do earthworms cause damage to paddy crop? *Mysore Journal of Agricultural Science* 23, 370–373.
- Ka Kayondo, J.K. (1984) Ecologie Alimentaire du Ver de Terre Detrivore *Millsonia lamtoiana* (Acanthodrilidae-Oligochaeta) dans la Savane de Lamto (Côte d'Ivoire). PhD Thesis, University of Paris VI, Paris, 121 pp.
- Kennel, W. (1990) The role of the earthworm *Lumbricus terrestris* in integrated fruit production. *Acta Horticulturae* 285, 149–156.
- Kobiyama, M. (1994) Influência da Minhoca Louca (*Amyntas* spp. Rosa, 1891) Sobre o Movimento da Água no Solo, Relacionado ao Crescimento da Bracatinga (*Mimosa scabrella* Benth.). PhD Thesis, Universidade Federal do Paraná, Curitiba.
- Kozlovskaya, L.S. and Zagurskaya, L.M. (1966) Über beziehungen zwischen regenwürmern und mikroben in Westsibirien. *Pedobiologia* 6, 244–257.
- Kozlovskaya, L.S. and Zhdannikova, E.N. (1961) The combined activity of earthworms and the microflora in forest soils. *Doklady Akademii Nauk, SSSR* 139, 574–576.
- Krishnamoorthy, R.V. and Vajranabahaiah, S.N. (1986) Biological activity of earthworm casts: an assessment of plant growth promoter levels in the casts. *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 95, 341–351.
- Lattaud, C., Locati, S., Mora, P., Rouland, C. and Lavelle, P. (1998) The diversity of digestive systems in tropical geophagous earthworms. *Applied Soil Ecology* 9, 189–195.
- Lavelle, P. (1971) Étude préliminaire de la nutrition d'un ver de terre africain *Millsonia anomala* (Acanthodrilidae, Oligochètes). In: d'Aguilar, J., Henriot, C.A., Bessard, A., Bouché, M.B. and Pussard, M. (eds) *Organismes du Sol et Production Primaire*. INRA, Paris, pp. 133–145.
- Lavelle, P. (1978) Les Vers de Terre de la Savane de Lamto (Côte d'Ivoire): Peuplements, Populations et Fonctions dans l'écosystème. Publications Laboratoire Zoologie, École Normale Supérieure, Paris, vol. 12.
- Lavelle, P. (1988) Earthworms and the soil system. *Biology and Fertility of Soils* 6, 237–251.
- Lavelle, P. (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Advances in Ecological Research* 24, 93–132.
- Lavelle, P. and Gilot, C. (1994) Priming effects of macroorganisms on microflora: a key process of soil function? In: Ritz, K., Dighton, J. and Giller, K. (eds) *Beyond the Biomass*. Wiley-Sayce, London, pp. 173–180.
- Lavelle, P., Zaidi, Z and Schaefer, R. (1989) Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. *Pedobiologia* 33, 379–388.
- Lavelle, P., Melendez, G., Pashanasi, B. and Schaefer, R. (1992) Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex corethrus* (Glossoscolecidae). *Biology and Fertility of Soils* 14, 49–53.
- López-Hernandez, D., Lavelle, P., Fardeau, J.C. and Niño, M. (1993) Phosphorus transformations in two P-sorption contrasting tropical soils during transit through *Pontoscolex corethrus* (Glossoscolecidae: Oligochaeta). *Soil Biology and Biochemistry* 25, 789–792.
- Loquet, M., Bhatnagar, T., Bouché, M.B. and Rouelle, J. (1977) Essai d'estimation de l'influence écologique des lombriciens sur les microorganismes. *Pedobiologia* 17, 400–417.

- Mulongoy, K. and Bedoret, A. (1989) Properties of worm casts and surface soils under various plant covers in the humid tropics. *Soil Biology and Biochemistry* 23, 609–617.
- Nardi, S., Panuccio, M. R., Abenavoli, M. R. and Muscolo, A. (1994) Auxin-like effect of humic substances extracted from faeces of *Allolobophora caliginosa* and *A. rosea*. *Soil Biology and Biochemistry* 26, 1341–1346.
- Németh, A. (1981) Estudio Ecológico de las Lombrices de Tierra (Oligochaeta) en Ecosistemas de Bosque Humedo Tropical en San Carlos de Rio Negro, Territorio Federal Amazonas. PhD Thesis, Universidad Central de Venezuela, Caracas. 92 pp.
- Niklas, J. and Kennel, W. (1981) The role of the earthworm, *Lumbricus terrestris* (L.) in removing sources of phytopathogenic fungi in orchards. *Gartenbauwissenschaft* 46, 138–142.
- Pani, S.C. (1986) Aspects of Ecological Studies of Tropical Earthworms in Irrigated Agricultural Systems of Orissa, India. PhD Thesis, Sambalpur University, Orissa, India. 232 pp.
- Pashanasi, B., Melendez, G., Szott, L. and Lavelle, P. (1992) Effect of inoculation with the endogeic earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on N availability, soil microbial biomass and the growth of three tropical fruit tree seedlings in a pot experiment. *Soil Biology and Biochemistry* 24, 1655–1659.
- Pashanasi, B., Alegre, J. and Lavelle, P. (1994) Efecto de lombrices de tierra (*Pontoscolex corethrurus*) sobre el crecimiento de cultivos anuales y características físicas y químicas en suelos de Yurimaguas. *Folia Amazonica* 6, 5–45.
- Pashanasi, B., Lavelle, P., Alegre, J. and Charpentier, F. (1996) Effect of the endogeic earthworm *Pontoscolex corethrurus* on soil chemical characteristics and plant growth in a low-input tropical agroecosystem. *Soil Biology and Biochemistry* 28, 801–810.
- Patrón, J.C. (1998) Dinámica del Fósforo en el Sistema Suelo-planta por Efecto de una Población de Lombrices Geófagas *Pontoscolex corethrurus*. MSc, Thesis, Colégio de Postgraduados, Montecillos, Mexico.
- Pederson, J.C. and Hendriksen, N.B. (1993) Effect of passage through the intestinal tract of detritore earthworms (*Lumbricus* spp.) on the number of selected Gram-negative and total bacteria. *Biology and Fertility of Soils* 16, 227–232.
- Pearce, T.G. (1978) Gut contents of some lumbricid earthworms. *Pedobiologia* 18, 153–157.
- Pearce, T.G., Roggero, N. and Tipping, R. (1994) Earthworms and seeds. *Journal of Biological Education* 28, 195–202.
- Puttarudriah, M. and Shivashankara-Sastry, K.S. (1961) A preliminary study of earthworm damage to crop growth. *Mysore Agricultural Journal* 36, 2–11.
- Reddell, P. and Spain, A.V. (1991a) Earthworms as vectors of viable propagules of mycorrhizal fungi. *Soil Biology and Biochemistry* 23, 767–774.
- Reddell, P. and Spain, A.V. (1991b) Transmission of infective *Frankia* (Actinomycetales) propagules in casts of the endogeic earthworm *Pontoscolex corethrurus* (Oligochaeta: Glossoscolecidae). *Soil Biology and Biochemistry* 23, 775–778.
- Rose, C.J. and Wood, A.W. (1980) Some environmental factors affecting earthworm populations and sweet potato production in the Tari Basin, Papua New Guinea highlands. *Papua New Guinea Agricultural Journal* 31, 1–13.
- Rouelle, J. (1983) Introduction of amoebae and *Rhizobium japonicum* into the gut of *Eisenia fetida* (Sav.) and *Lumbricus terrestris* L. In: Satchell, J.E. (ed.)

- Earthworm Ecology: From Darwin to Vermiculture*. Chapman and Hall, New York, pp. 375–381.
- Satchell, J.E. and Martin, K. (1984) Phosphatase activity in earthworm faeces. *Soil Biology and Biochemistry* 16, 191–194.
- Senapati, B.K. and Dash, M.C. (1981) Effect of grazing on the elements of production in vegetation and Oligochaete components of a tropical pasture. *Revue d'Écologie et Biologie du Sol* 18, 487–505.
- Senapati, B.K., Pani, S.C. and Kabi, A. (1985) Effect of earthworm and green manuring on paddy. *Proceedings of the Soil Biology Symposium*, Hisar, India, February 1985, pp. 71–75.
- Shumway, D.L. and Koide, R.T. (1994) Seed preferences of *Lumbricus terrestris* L. *Applied Soil Ecology* 1, 11–15.
- Simek, M. and Pizl, V. (1989) The effect of earthworms (Lumbricidae) on nitrogenase activity in the soil. *Biology and Fertility of Soils* 7, 370–373.
- Spain, A.V., Safigna, P.G. and Wood, A.W. (1990) Tissue carbon sources for *Pontoscolex corethrurus* (Oligochaeta, Glossoscolecidae) in a sugarcane ecosystem. *Soil Biology and Biochemistry* 22, 703–706.
- Spain, A.V., Lavelle, P. and Mariotti, A. (1992) Stimulation of plant growth by tropical earthworms. *Soil Biology and Biochemistry* 24, 1629–1633.
- Stephens, P.M. and Davoren, C.W. (1995) Effect of the lumbricid earthworm *Aporrectodea trapezoides* on wheat grain yield in the field, in the presence or absence of *Rhizoctonia solani* and *Gaeumannomyces graminis* var. *tritici*. *Soil Biology and Biochemistry* 28, 561–567.
- Stephens, P.M., Davoren, C.W., Ryder, M.H. and Doube, B.M. (1993) Influence of the lumbricid earthworm *Aporrectodea trapezoides* on the colonization of wheat roots by *Pseudomonas corrugata* strain 2140R in soil. *Soil Biology and Biochemistry* 25, 1719–1724.
- Stephens, P.M., Davoren, C.W., Ryder, M.H. and Doube, B.M. (1994a) Influence of the earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* on *Rhizoctonia solani* disease of wheat seedlings and the interaction with a surface mulch of cereal-pea straw. *Soil Biology and Biochemistry* 26, 1285–1287.
- Stephens, P.M., Davoren, C.W., Doube, B.M. and Ryder, M.H. (1994b) Ability of the lumbricid earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* to reduce the severity of take-all under greenhouse and field conditions. *Soil Biology and Biochemistry* 26, 1291–1297.
- Stephens, P.M., Davoren, C.W., Ryder, M.H. and Doube, B.M. (1994c) Influence of the earthworm *Aporrectodea trapezoides* (Lumbricidae) on the colonization of alfalfa (*Medicago sativa* L.) roots by *Rhizobium meliloti* strain L5-30R and the survival of *Rhizobium meliloti* L5-30R in soil. *Biology and Fertility of Soils* 18, 63–70.
- Striganova, B. R. (1982) Determination of food ration in the earthworms *Nicodrilus caliginosus*. *Doklady Akademii Nauk SSSR* 266, 500–503.
- Striganova, B. R. (1984) Feeding of *Eisenia nordenskioldi* earthworms in SubArctica. *Doklady Akademii Nauk SSSR* 284, 253–256.
- Striganova, B.R., Derimova, T.D.P., Mazantseva, G.P. and Tiunov, A.V. (1989) Effects of earthworms on biological nitrogen fixation in the soil. *Biological Bulletin of the Academy of Sciences, USSR* 15, 560–565.
- Syers, J.K. and Springett, J.A. (1984) Earthworms and soil fertility. *Plant and Soil* 76, 93–104.

- Thompson, K., Green, A. and Jewels, A.M. (1994) Seeds in soil and worm casts from a neutral grassland. *Functional Ecology* 8, 29–35.
- Thompson, L., Thomas, C.D., Radley, J.M.A., Williamson, S. and Lawton, J.H. (1993) The effects of earthworms and snails in a simple plant community. *Oecologia* 95, 171–178.
- Tomati, U. and Galli, E. (1995) Earthworms, soil fertility and plant productivity. *Acta Zoologica Fennica* 196, 11–14.
- Tomati, U., Grappelli, A. and Galli, E. (1988) The hormone-like effect of earthworm casts on plant growth. *Biology and Fertility of Soils* 5, 288–294.
- Tomati, U., Galli, E., Grappelli, A. and Di Lena, G. (1990) Effect of earthworm casts on protein synthesis in radish (*Raphanus sativum*) and lettuce (*Lactuca sativa*) seedlings. *Biology and Fertility of Soils* 9, 288–289.
- Tomati, U., Galli, E. and Pasetti, L. (1996) Effect of earthworms on molybdenum-dependent activities. *Biology and Fertility of Soils* 23, 359–361.
- van der Reest, P.J. and Rogaar, H. (1988) The effect of earthworm activity on the vertical distribution of plant seeds in newly reclaimed polder soils in the Netherlands. *Pedobiologia* 31, 211–218.
- Waters, R.A.S. (1951) Earthworms and the fertility of pasture. *Proceedings of the New Zealand Grassland Association* 13, 168–175.
- Ydrogo, H.F.B. (1994) Efecto de las Lombrices de Tierra (*Pontoscolex corethrurus*) en las Micorrizas Vesiculo Arbusculares (M.V.A.) en la Etapa de Crecimiento de Arazá (*Eugenia stipitata*), Achiote (*Bixa orellana*), Pijuayo (*Bactris gasipaes*), en Suelos Ultisoles de Yurimaguas. Undergraduate Thesis, Universidad Nacional de San Martín, Tarapoto, Peru. 80 pp.
- Zou, X. (1992) Phosphorus Transformation in Soils: a New Method and Tree Species Effects. PhD Thesis, Colorado State University, USA.

Appendix 4.1.

Country	Location	Crop	Earthworm species	Residues (kg m ⁻²)	Plot size (m ²)	Grain yield (t ha ⁻¹)			Shoot yield (t ha ⁻¹)		
						Control	Worm	% Increase ^a	Control	Worm	% Increase ^a
Ivory Coast	Lamto	Yam	<i>M. anomala</i>	0.25	0.72				0.72	0.96	33.79
Ivory Coast	Lamto	Yam	<i>M. anomala</i>	0	0.72				0.47	0.58	24.18
Ivory Coast	Lamto	Yam	<i>M. anomala</i>	0.4	0.72				0.27	0.35	30.21
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	3.52	3.45	-2.00	6.62	5.94	-10.27
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.25	1.28	3.40	3.35	-1.38	6.71	6.84	1.94
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	1.09	1.16	5.71	1.95	2.04	4.62
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.63	1.28	1.28	1.03	-19.51	2.25	2.07	-8.00
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	1.70	1.80	5.99	3.14	3.38	7.64
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.31	1.28	1.67	1.98	18.22	3.03	3.09	1.98
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	1.65	1.26	-23.70	3.20	2.98	-6.88
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.35	1.28	1.51	1.81	20.21	3.25	3.40	4.62
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	1.23	1.30	5.70	3.09	3.84	24.27
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.5	1.28	0.94	1.24	32.50	2.87	2.91	1.39
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	1.28	0.61	0.74	21.79	1.63	1.77	8.59
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.34	1.28	0.55	0.66	21.43	1.41	1.64	16.31
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0.16	0.72	3.02	3.57	18.23	3.67	3.44	-6.27
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64	2.10	2.68	27.62	19	19	0
Mexico	La Mancha	Maize	<i>P. corethrus</i>	1.12	0.64	2.23	2.45	9.87	11	12	9.09
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64				7.8	8.2	5.13
Mexico	La Mancha	Maize	<i>P. corethrus</i>	2	0.64				9.5	9.2	-3.16
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64				2.1	2.2	4.76
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0.92	0.64				3.1	3.3	6.45
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64	2.13	2.02	-5.16	5.2	6.5	25.00
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0.33	0.64	2.00	2.05	2.50	5.7	7	22.81
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64	1.00	1.43	43.00	19	20	5.26
Mexico	La Mancha	Maize	<i>P. corethrus</i>	1.2	0.64	1.35	1.51	11.85	14	12	-14.29
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0	0.64	0.84	1.48	76.19	7	7.7	10.00
Mexico	La Mancha	Maize	<i>P. corethrus</i>	0.77	0.64	1.59	1.52	-4.40	8.4	8.4	0
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0	0.28	1.09	1.53	40.37	1.89	2.52	33.33
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.25	0.28	1.22	1.70	39.34	2.55	2.65	3.92
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.43	0.28	1.62	2.13	31.48	2.05	3.12	52.20
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0	0.28	0.77	1.57	103.90	1.28	2.13	66.41
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.25	0.28	0.78	1.62	107.69	2.09	1.8	-13.88
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.56	0.28	0.95	1.49	56.84	1.31	2.71	106.87
Peru	Yurimaguas	Cowpea	<i>P. corethrus</i>	0	0.28	0.84	0.85	1.19	1.23	1.16	-5.69
Peru	Yurimaguas	Cowpea	<i>P. corethrus</i>	0.21	0.28	0.91	0.78	-14.29	1.28	1.86	45.31
Peru	Yurimaguas	Cowpea	<i>P. corethrus</i>	0.52	0.28	1.24	1.22	-1.61	1.52	1.69	11.18
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0	0.28	0.73	1.12	53.42	1.56	2.71	73.72
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.12	0.28	1.02	1.53	50.00	2.35	2.6	10.64
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.32	0.28	1.39	2.00	43.88	2.32	3.14	35.34
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0	0.28	0.86	0.71	-17.44	1.39	0.98	-29.50
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.27	0.28	1.16	0.66	-43.10	1.09	1.92	76.15
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.56	0.28	1.59	0.95	-40.25	1.88	1.23	-34.57
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0	0.28	0.30	0.94	213.33	0.98	2.82	187.76
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.1	0.28	1.10	1.21	10.00	1.82	3.22	76.92
Peru	Yurimaguas	Rice	<i>P. corethrus</i>	0.37	0.28	1.70	1.95	14.71	2.64	4.08	54.55
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.25	0.28	1.18	1.49	26.96	2.51	2.85	13.63
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.29	0.28	0.66	2.90	341.19	2.6	2.9	11.78
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.29	0.28	0.12	0.78	525.00	1.85	2.68	44.96
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.28	0.28	0.83	0.53	-36.42	1.6	2.14	33.54
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.21	0.28	1.86	2.89	54.99	5.23	7.13	36.32
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.71	0.28	1.36	2.44	79.21	2.02	2.48	22.56
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.25	0.28	0.00	0.09		4.81	3.66	-23.89
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.37	0.28	2.36	2.80	18.80	4.62	3.81	-17.51
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	0.38	0.28	2.37	1.94	-18.07	4.83	3.94	-18.48
Peru	Yurimaguas	Maize	<i>P. corethrus</i>	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	3.86	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.

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

Appendix 4.1. *Continued.*

Country	Location	Crop	Earthworm species	Residues (kg m ⁻²)	Plot size (m ²)	Grain yield (t ha ⁻¹)			Shoot yield (t ha ⁻¹)		
						Control	Worm	% Increase ^a	Control	Worm	% Increase ^a
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	0.04				0.16	0.65	309.52
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	0.04				0.16	0.26	65.08
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	0.04				0.16	0.59	273.02
Ivory Coast	Lamto	Maize	<i>P. corethrurus</i>	0	0.04				0.16	0.34	112.70
Ivory Coast	Lamto	Maize	<i>H. africanus</i>	0	0.04				0.16	0.20	28.57
Ivory Coast	Lamto	Maize	<i>S. porilera</i> + <i>C. zielae</i>	0	0.04				0.16	0.30	92.06
Ivory Coast	Lamto	<i>Panicum maximum</i>	<i>M. anomala</i>	0	0.04				0.94	1.70	81.78
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				0.94	2.36	151.76
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				0.94	2.35	150.37
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				0.94	3.25	247.07
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				0.94	2.72	190.26
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				6.66	10.08	51.41
Ivory Coast	Lamto	<i>P. maximum</i>	<i>M. anomala</i>	0	0.04				6.66	5.97	-10.29
Ivory Coast	Lamto	<i>P. maximum</i>	<i>S. porilera</i> + <i>C. zielae</i>	0	0.04				0.94	1.75	86.23
Ivory Coast	Lamto	<i>P. maximum</i>	<i>S. porilera</i> + <i>C. zielae</i>	0	0.04				0.94	2.94	214.03
Ivory Coast	Lamto	Rice	<i>S. porilera</i> + <i>C. zielae</i>	0	0.053	1.24	1.09	-11.99	1.55	1.86	7.10
Ivory Coast	Lamto	Rice	<i>H. africanus</i>	0	0.053	1.24	1.28	3.19	1.55	1.42	-8.39
Ivory Coast	Lamto	Rice	<i>M. anomala</i>	0	0.053	1.24	1.21	-2.43	1.55	1.59	2.58
Ivory Coast	Lamto	Rice	<i>M. anomala et al.</i>	0	0.053	1.24	1.51	21.70	1.55	1.76	13.55
Ivory Coast	Lamto	Peanuts	<i>S. porilera</i> + <i>C. zielae</i>	0	0.053	2.32	1.68	-27.72	2.92	3.04	4.11
Ivory Coast	Lamto	Peanuts	<i>H. africanus</i>	0	0.053	2.32	1.82	-21.71	2.92	2.87	-1.71
Ivory Coast	Lamto	Peanuts	<i>M. anomala</i>	0	0.053	2.32	1.73	-25.45	2.92	3.18	8.90
Ivory Coast	Lamto	Peanuts	<i>M. anomala et al.</i>	0	0.053	2.32	2.18	-6.26	2.92	3.02	3.42
Ivory Coast	Lamto	Maize	<i>S. porilera</i> + <i>C. zielae</i>	0	0.053	0.17	0.20	19.32	3.34	3.71	11.08
Ivory Coast	Lamto	Maize	<i>H. africanus</i>	0	0.053	0.17	0.26	54.55	3.34	3.65	9.28
Ivory Coast	Lamto	Maize	<i>M. anomala</i>	0	0.053	0.17	0.42	152.27	3.34	4.66	39.52
Ivory Coast	Lamto	Maize	<i>M. anomala et al.</i>	0	0.053	0.17	0.50	201.14	3.34	4.12	23.35
Mexico	La Vibora	Beans	<i>P. corethrurus</i>	0	0.009				0.17	0.19	8.28
Mexico	La Vibora	Beans	<i>P. elongata</i>	0	0.009				0.17	0.16	-8.92
Mexico	La Vibora	Beans	<i>P. corethrurus</i>	0	0.064				0.14	0.19	33.33
Mexico	La Vibora	Beans	<i>P. elongata</i>	0	0.064				0.14	0.34	144.44
Mexico	La Vibora	Beans	<i>P. corethrurus</i>	0	0.064	0.06	0.07	25.97	0.08	0.17	112.50
Mexico	La Vibora	Beans	<i>P. elongata</i>	0	0.064	0.06	0.06	1.66	0.08	0.2	150.00
Mexico	Los Tuxtlas	Maize	<i>P. corethrurus</i>	0	0.064	2.58	3.16	22.42	15.84	14.19	-10.42
Mexico	Los Tuxtlas	Maize	<i>P. corethrurus</i>	0.14	0.064	3.44	1.53	-55.51	13.55	10.58	-21.9
Mexico	Los Tuxtlas	Maize	<i>P. corethrurus</i>	0	0.009				0.94	0.81	-14.61
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				0.27	0.30	8.57
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				4.12	3.72	-9.68
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				0.24	0.20	-16.18
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				0.59	0.57	-4.40
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				2.91	2.73	-6.20
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.064				3.22	1.10	-65.80
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.049				0.67	0.81	21.21
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.049				0.47	0.63	34.78
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.049				6.49	5.02	-22.57
Mexico	La Vibora	<i>B. decumbens</i>	<i>P. corethrurus</i>	0	0.049				4.14	6.21	50.25
Peru	Yurimaguas	<i>Bixa orellana</i>	<i>P. corethrurus</i>	0	0.036				0.1486	1.8708	1158.87
Peru	Yurimaguas	<i>B. orellana</i>	<i>P. corethrurus</i>	0	0.036				3	9	
Peru	Yurimaguas	<i>B. orellana</i>	<i>P. corethrurus</i>	0	0.036				0.15	1.64	1000.56
Peru	Yurimaguas	<i>B. orellana</i>	<i>P. corethrurus</i>	0	0.036				0.80	1.64	106.78
Peru	Yurimaguas	<i>B. orellana</i>	<i>P. corethrurus</i>	0	0.036				0.80	2.23	180.48
Peru	Yurimaguas	<i>Baccharis gasipaes</i>	<i>P. corethrurus</i>	0	0.036				0.80	0.46	-42.04
Peru	Yurimaguas	<i>B. gasipaes</i>	<i>P. corethrurus</i>	0	0.036				0.80	0.31	-60.74
Peru	Yurimaguas	<i>B. gasipaes</i>	<i>P. corethrurus</i>	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	86.31	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.

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

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

^a% increase = (worm - control)/Control.

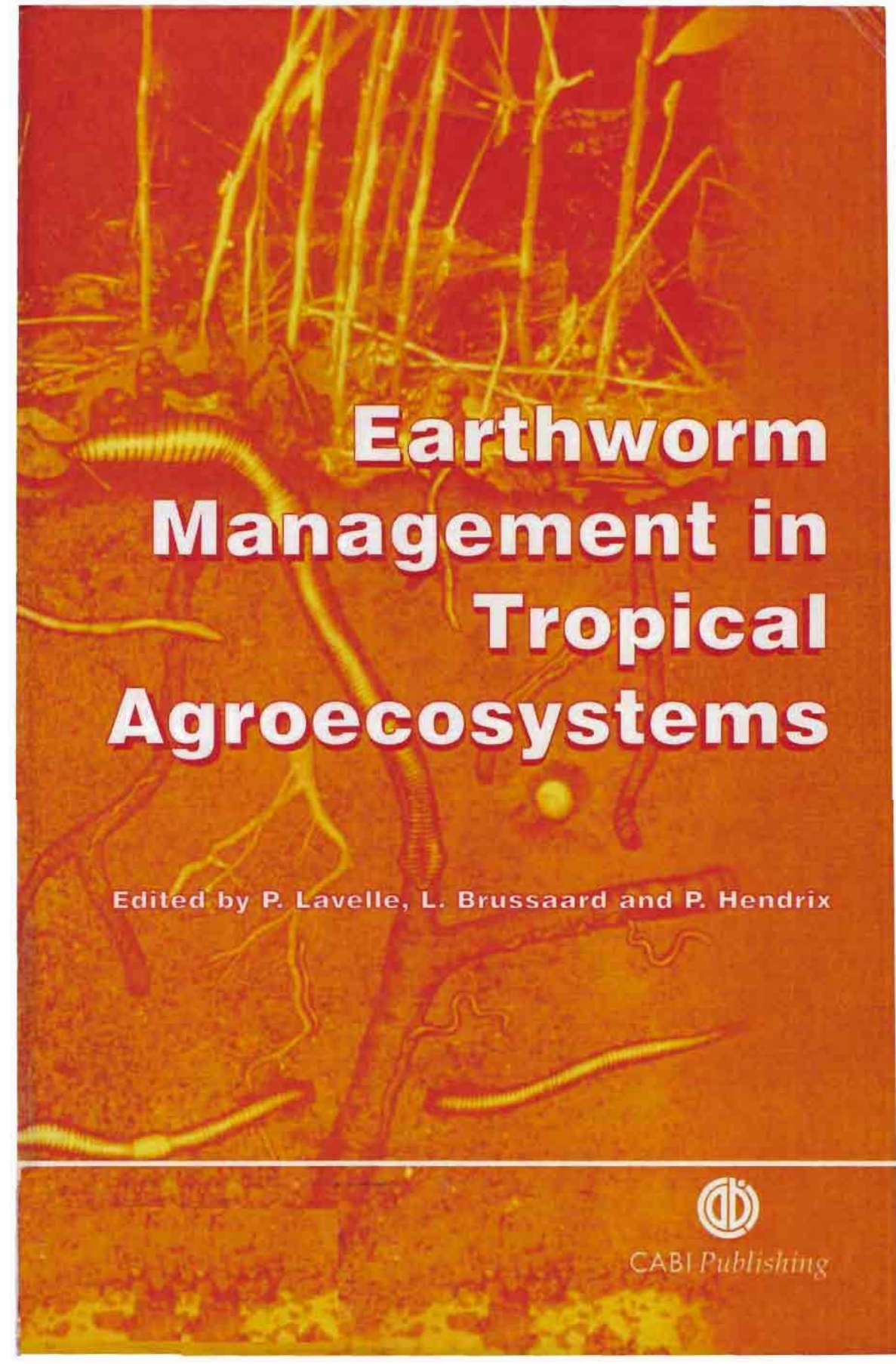
^b% survival = 1 + [(Final earthworm mass - Initial earthworm mass)] / Initial earthworm mass.

^cMass difference = final earthworm mass in inoculated plot - mass in uninoculated plot.

^dSeveral species (unidentified) were added.

^eNot significantly different.

Root yield (t ha ⁻¹)			Shool/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

The cover features a detailed illustration of a soil profile. At the top, there are plant roots extending downwards. In the middle section, a large earthworm is shown in profile, moving through the soil. Below it, a smaller nematode is visible. The background is a textured, brownish-orange color representing soil.

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