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

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Summary

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

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

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

Introduction

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

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

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

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

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

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

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

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

Demographic Parameters

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

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

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

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

Table 3.2b.

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

[a]Pigmentation: 0 = none; + anterior, ++, antero-dorsal; +++ whole body. [b]Unpublished data. [c]Data from Senapati (1980) or Senapati and Sahu (1993 a,b) and Senapati et al. (1993, 1995, unpublished data)
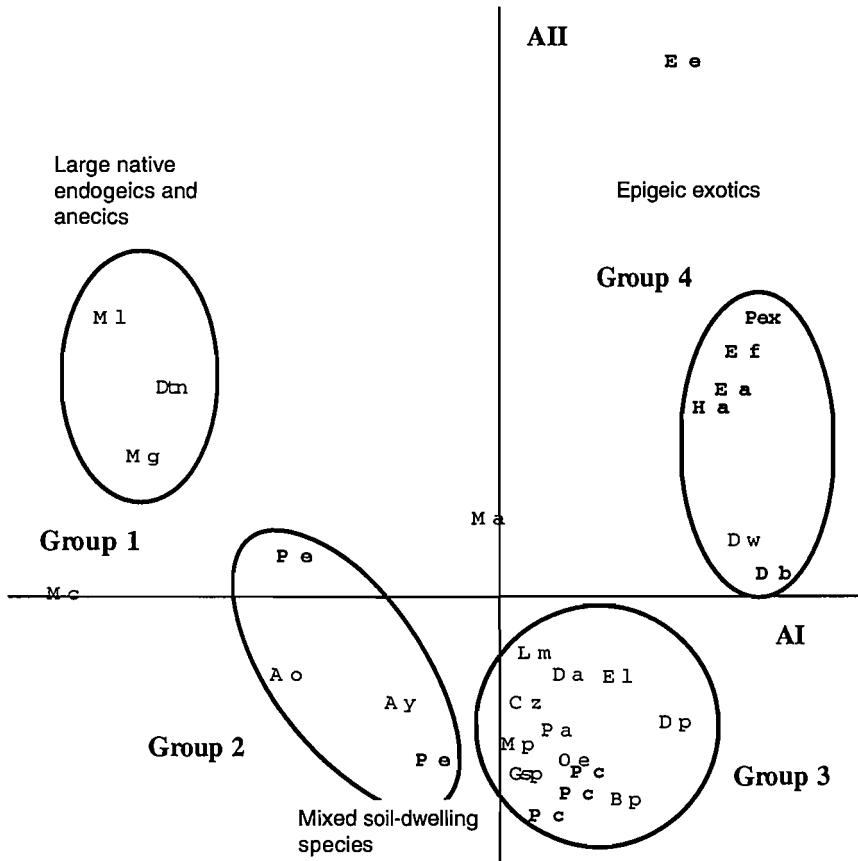
populations live and fecundity number of hatchlings per cocoon, respectively. A cluster analysis allowed separation of four major groups of species (Fig. 3.2):

1. Group 1 comprises large endogeic and anecic native species (12–32 g fresh wt) with a long generation time of 2–4 years, low fecundity (0.5–3.1 cocoons year^{-1} adult^{-1}) and only one hatchling per cocoon.

2. Group 2 is rather heterogeneous and comprises medium size species (1.2–6 g), with fecundity of 1.3–45, and generally one hatchling per cocoon except for *P. elongata* (1.2).

3. Group 3 contains a large number of endogeic species of relatively small size (170–1250 mg), with generation time of 3–7 months for most species, except *D. agilis* (15 months) and *C. zielae* (18 months), intermediate fecundity of 10–25 cocoons adult^{-1} year^{-1}, except for *P. corethrurus* (up to 68), *E. lavellei*

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

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

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

4. Group 4 is the opposite to group 1; it contains six species that are mainly exotic epigeic, four of them being used for vermicomposting. These species are generally small (80–550 mg) have short generation times (1–3 months), high
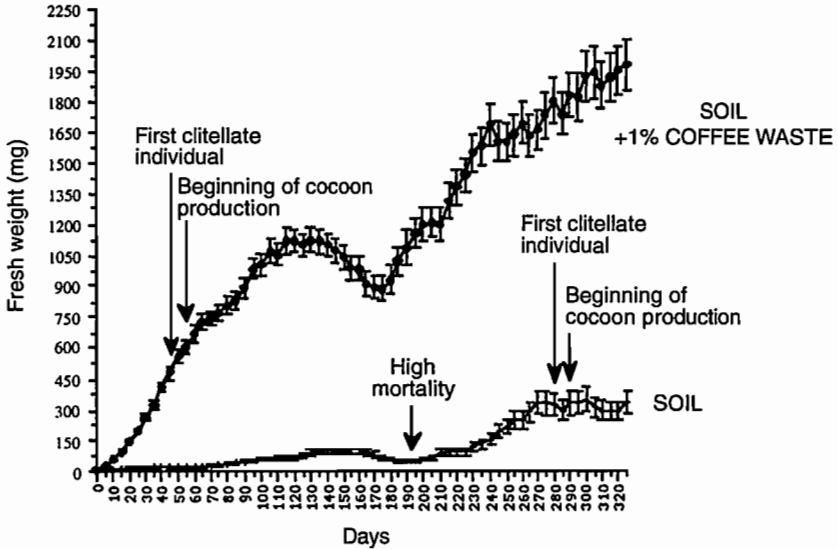
Fig. 3.3. Growth of *Hyperiodrilus africanus* in control soil and soil enriched with 1% coffee waste (Tondoh, 1994).

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

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

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

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

In field conditions, demographic parameters may vary considerably depending on soil moisture and organic content. At Lamto (Ivory Coast), for instance, *H. africanus* can only grow if the soil of the upper 10 cm is supplemented with organic residues. Growth and fecundity then depend on soil moisture and the quality of the residue (Fig. 3.3, Tondoh, 1994) or the soil organic
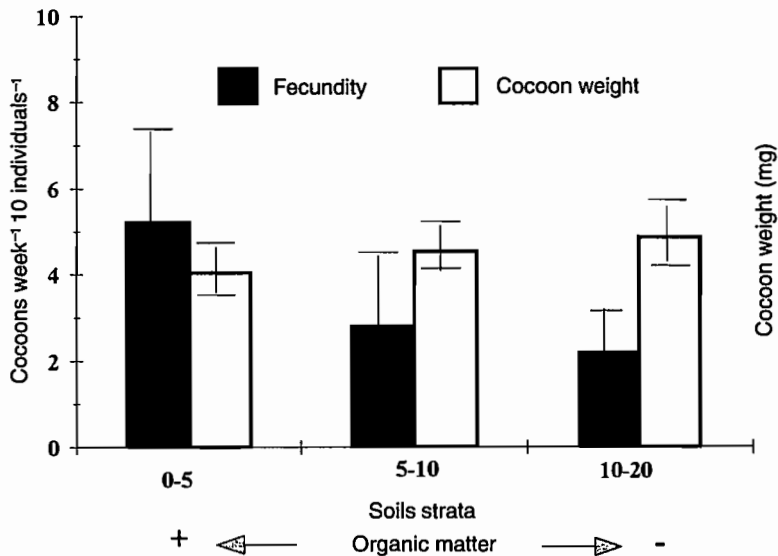
Fig. 3.4. Fecundity and cocoon weight of *Balanteodrilus pearsei* from La Mancha (Mexico) grown in three soil strata (from Angeles, 1996).

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

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

Therefore, technologies using these earthworms will be limited to regions with temperatures above 20°C and annual rainfall >1000–1200 mm. More generally speaking, the availability of organic matter or residues to feed the worms is often a major limitation to earthworm activities in agroecosystems where organic stocks may be highly depleted. For example, growth of *P. elongata* at St Anne (Martinique) is highly limited in soils subjected to intensive market gardening (Blanchart, 1997); in that case, a dramatic decrease in
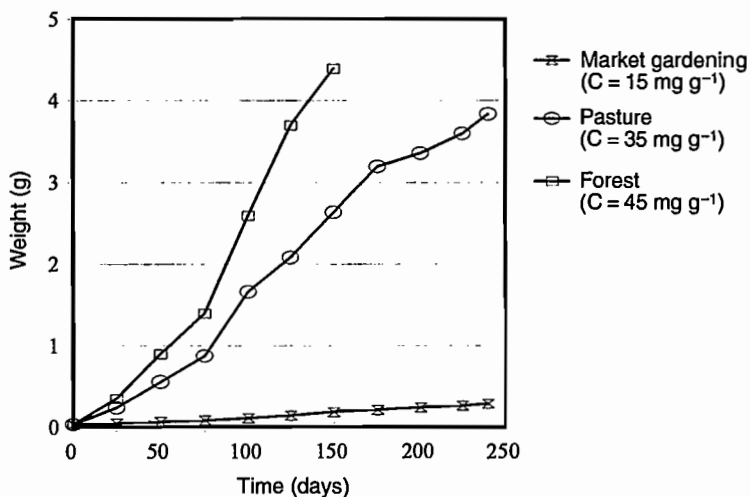
Fig. 3.5. Comparative growth of *Poypheretima elongata* in Vertisols with different C contents (Blanchart *et al.*, unpublished data).

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

Spatial Distribution Patterns

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

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

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

Species	Taylor's index b values	Standard error
Agastrodrilus opisthogynus	1.140	0.13
Millsonia anomala	1.626	0.221
Dichogaster terrae nigrae	1.121	0.069
Millsonia ghanensis	1.025	0.076
Millsonia lamtoiana	1.026	0.007
Chuniodrilus zielae	1.724	0.169
Dichogaster agilis	1.324	0.084
Balanteodrilus pearsei	1.3	0.1
Onychochaeta elegans	2.12	0.08
Ocnerodrilus occidentalis	1.22	0.2
Pontoscolex corethrurus	1.63	0.11
Polypheretima elongata	1.87	0.12
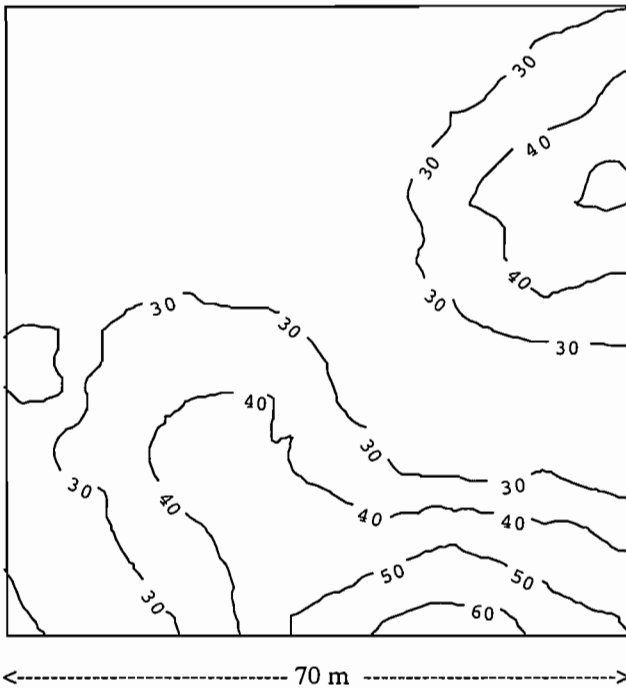
Fig. 3.6. Horizontal distribution of small polyhumic *Glossodrilus sikuania* in *Brachiaria decumbens* + *Pueraria phaseoloides* pasture at Carimagua (Colombia) in the Oriental llanos (November, 1994) in a 70 × 70m square plot. Contours represent earthworm density (ind m^{-2}).

Soil Ingestion Rates and Particle Size Selection

Ingestion rates

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

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

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

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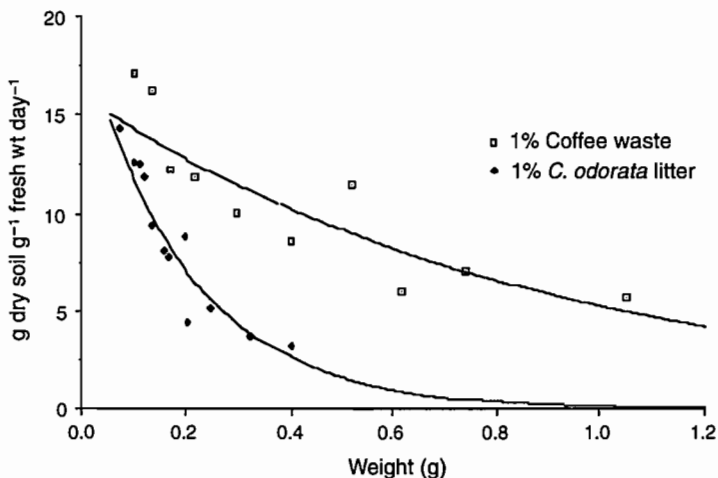

Fig. 3.7. Soil ingestion rate of *Hyperiodrilus africanus* as a function of individual weight in soil enriched with 1% litter of *Chromolaena odorata* and 1% coffee waste (Tondoh, 1994).

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

Cast shape

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

Selection of organic and mineral size particles

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

Epigeics ingest mainly litter. Anecics ingest a mixture of litter and mineral soil. For example, the large African anecic *M. lamtoiana* ingests a mixture of 12% coarse organic debris and 88% soil (Kanyonyo, 1984). Guggenberger
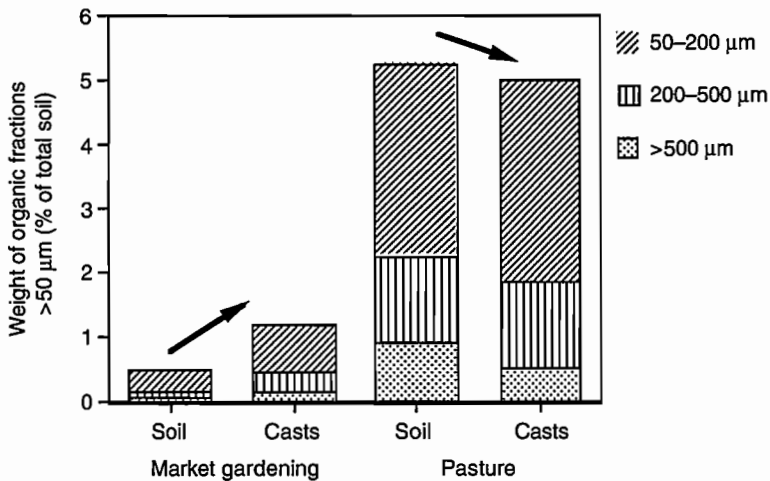
Fig. 3.8. Weight percentage of organic fractions >50 μm in casts of *Polypheretima elongata* and control vertisols from two systems in Martinique (Duboisset, 1994).

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

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

P. elongata from Martinique exhibited the largest number of enzymes secreted by its gut tissue. For *M. anomala* and *P. corethrurus*, the origin of most enzymes, such as cellulase and mannase, was microbial and not the gut itself. These results support the hypothesis of a mutualistic earthworm–microflora
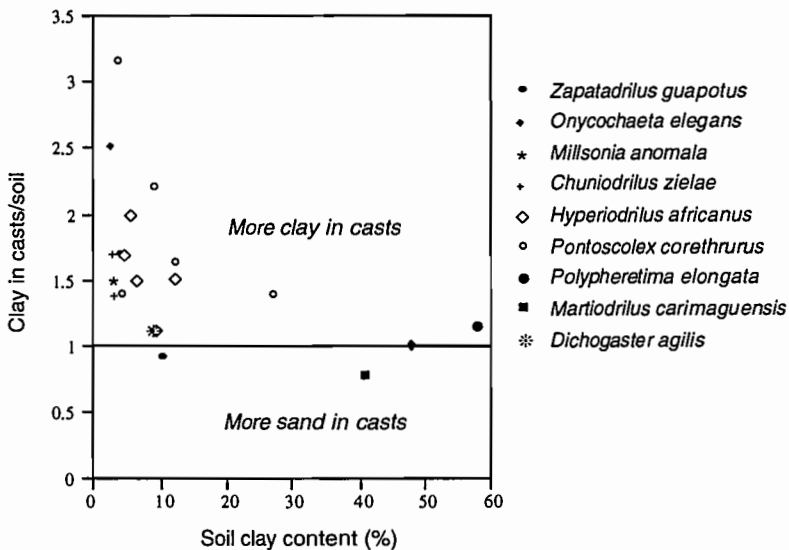
Fig. 3.9. Effects of soil clay content on selective ingestion of clay particles by different earthworm species.

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

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

Microorganisms, mycorrhizae and seed dispersion

Brown (1995), in his extensive review, suggested that the interactions between microorganisms and earthworms have more beneficial than negative effects. Earthworm feeding leads to a digestion, an activation and stimulation of selected microorganisms (Barois, 1987). They can also passively disperse propagules, spores and seeds.
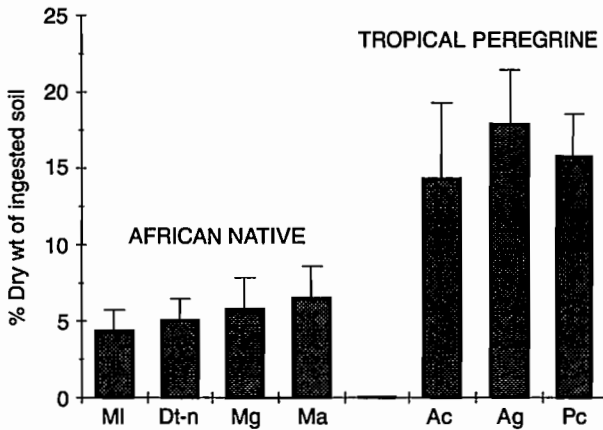
Fig. 3.10.   Proportion of intestinal mucus added to the ingested soil by selected species of earthworm (after Lavelle *et al.,* 1983; Martin *et al.,* 1987; Barois, 1992). Ac = *Amynthas corticis,* Ag = *Amynthas gracilis,* Dt-n = *Dichogaster terrae-nigrae,* Ma = *Millsonia anomala,* Mg = *Millsonia ghanensis,* Ml = *Millsonia anomala,* Pc = *Pontoscolex corethrurus.*

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

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

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

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

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

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

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

Nitrogen

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

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

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

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

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

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

Other nutrients

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

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

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

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

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

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

Phosphorus

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

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

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

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

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

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

Conclusion

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

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

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

However, one of the most difficult parameter to determine for a successful earthworm population growth is its food, particularly for mesohumic and

oligohumic species. Some of the selected species with environmental tolerance, found in natural and managed ecosystems, were hard to cultivate in laboratory conditions, e.g. *M. anomala* (Ivory Coast), *Z. guapotus* (Mexico) and *R. pashanasi* (Peru). Some work needs to be done in this direction.

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

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

Short-term effects of earthworms on soil include:

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

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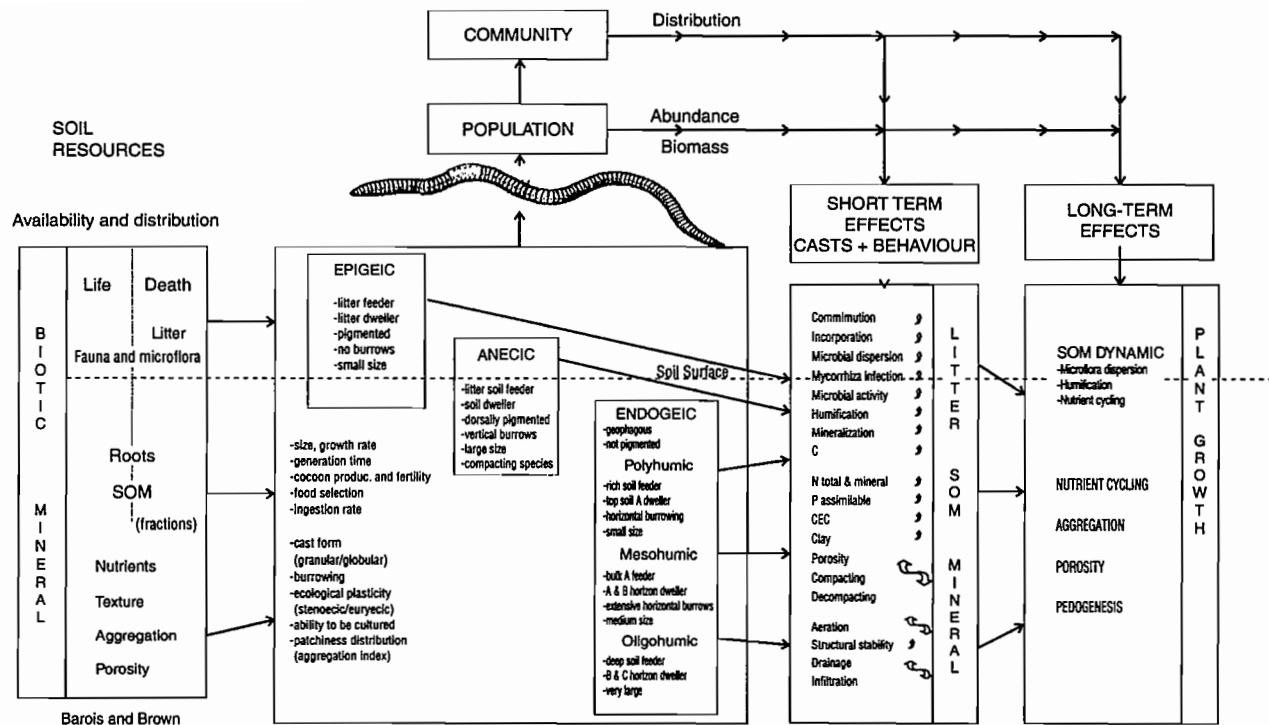
COMMUNITY — Distribution

POPULATION — Abundance / Biomass

SOIL RESOURCES

Availability and distribution

SHORT TERM EFFECTS CASTS + BEHAVIOUR

LONG-TERM EFFECTS

BIOTIC

Life | Death

Litter

Fauna and microflora

Roots

SOM

(fractions)

MINERAL

Nutrients

Texture

Aggregation

Porosity

Barois and Brown

EPIGEIC
- litter feeder
- litter dweller
- pigmented
- no burrows
- small size

ANECIC
- litter soil feeder
- soil dweller
- dorsally pigmented
- vertical burrows
- large size
- compacting species

Soil Surface

ENDOGEIC
- geophagous
- not pigmented

Polyhumic
- rich soil feeder
- top soil A dweller
- horizontal burrowing
- small size

Mesohumic
- bulk A feeder
- A & B horizon dweller
- extensive horizontal burrows
- medium size

Oligohumic
- deep soil feeder
- B & C horizon dweller
- very large

- size, growth rate
- generation time
- cocoon produc. and fertility
- food selection
- ingestion rate

- cast form (granular/globular)
- burrowing
- ecological plasticity (stenoecic/euryecic)
- ability to be cultured
- patchiness distribution (aggregation index)

Commimution
Incorporation
Microbial dispersion
Mycorrhiza infection
Microbial activity
Humification
Mineralization
C

N total & mineral
P assimilable
CEC
Clay
Porosity
Compacting
Decompacting

Aeration
Structural stability
Drainage
Infiltration

LITTER SOM MINERAL

SOM DYNAMIC
- Microflora dispersion
- Humification
- Nutrient cycling

NUTRIENT CYCLING

AGGREGATION

POROSITY

PEDOGENESIS

PLANT GROWTH

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

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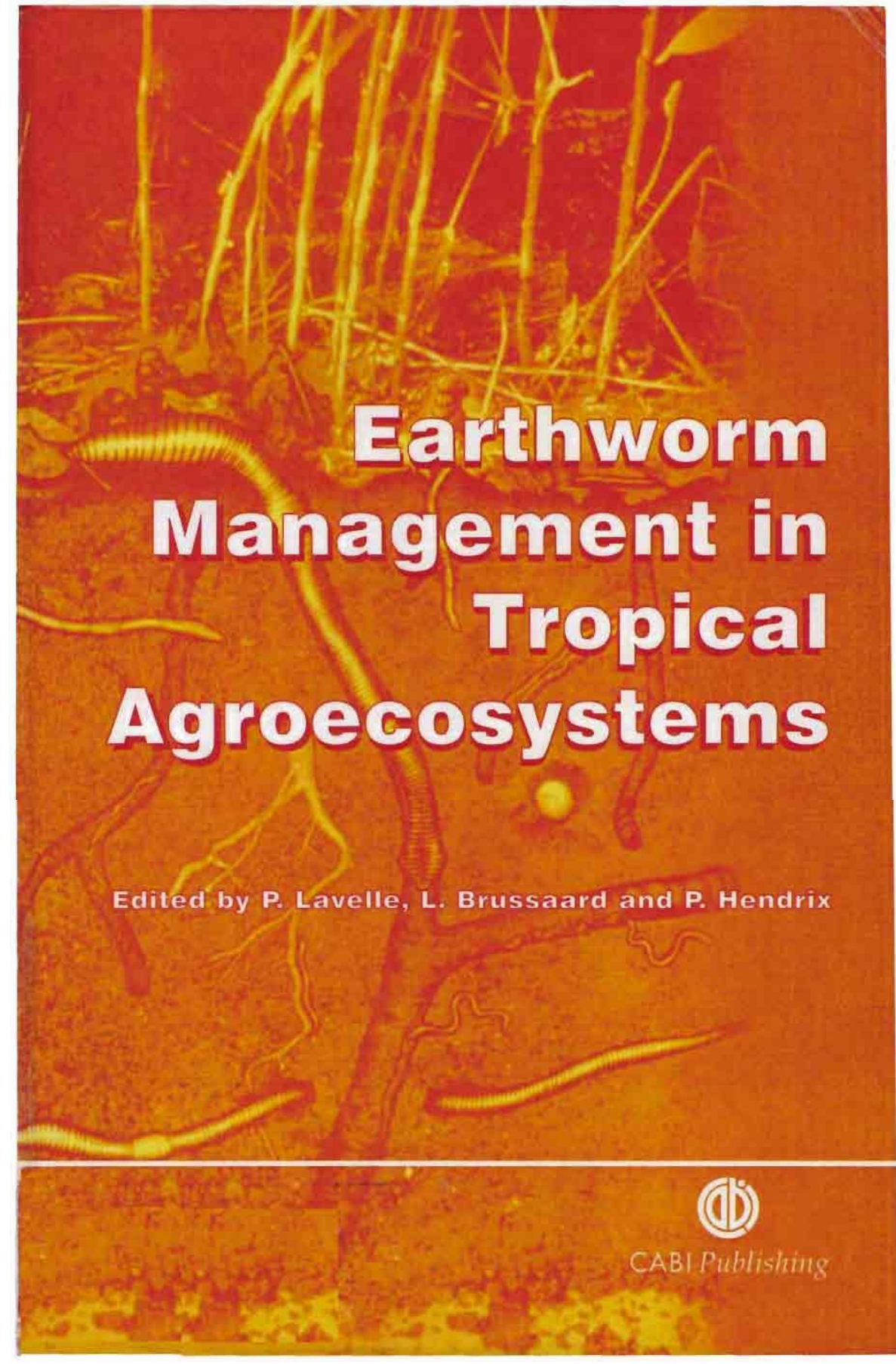
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