SMALL-SCALE AND LARGE-SCALE EFFECTS OF ENDOGEIC EARTHWORMS ON SOIL ORGANIC MATTER DYNAMICS IN SOILS OF THE HUMID TROPICS

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Summary—The effects of endogeic earthworms on the soil organic matter (SOM) dynamics of moist tropical soils are: (i) a sharp increase of mineralization during digestion; (ii) the presence in fresh casts of large amounts of mineral nutrients which are reorganized in microbial biomass at the scale of days to weeks depending on soil properties; (iii) a subsequent blocking of mineralization at the scale of months to years in the compact structure of ageing casts (i.e. older than 1–2 weeks).

It is hypothesized that, at the larger scale of soil profile and years, activities of earthworms will result in an acceleration of SOM turnover and the accumulation of labile rather than passive organic matter.

INTRODUCTION

In the humid tropics earthworms may have a predominant effect on regulation of soil organic matter dynamics. In situations where neither climatic conditions, humid and warm, nor clay minerals, little active and sometimes little abundant, can efficiently regulate mineralization biological regulations become predominant (Uehara, 1982; Swift *et al.*, 1979; Oades *et al.*, 1989; Lavelle, 1987; Anderson and Flanagan, 1989; Lavelle *et al.*, 1992). Such regulations operate in four main mutualistic associations of "macro-organisms" (i.e. macroinvertebrates and roots) with microorganisms.

(1) The litter system in which the energy source is represented by leaf and woody litter, arthropod communities are the main invertebrate components and the microflora is mainly represented by fungi; surface roots which grow among the leaves act as a sink for the nutrients released through decomposition.

(2) The rhizosphere is a centre of very active mutualistic interactions among roots, microflora (free bacteria, nitrogen-fixing bacteria and mycorrhizae) and associated microfauna; which result in the release of nutrients from soil organic matter (SOM).

(3) The "termitosphere" comprises termites and the whole part of soil and litter that they affect, in cooperation with a suite of obligate or transient mutualistic microorganisms.

(4) The drilosphere is defined as earthworms and the entire volume of soil and litter that they influence through their activities, in mutualistic association with free soil microorganisms and, possibly, a few obligate symbiotic protozoa or bacteria (Rouelle *et al.*, 1985).

The drilosphere system associates endogeic or anecic earthworms with free-living soil bacteria. In the case of tropical endogeic species, it has been demonstrated that the addition to the ingested soil of water (+100% of the dry weight of soil) and readily assimilable intestinal mucus (6–18% depending on the species) rapidly stimulates microbial activity. In the second half of the gut, the mucus has been almost entirely metabolized and microorganisms start to degrade soil organic matter into assimilable organic matter which is used by the worm and microorganisms, and nutrients are made available to plants (Barois and Lavelle, 1986; Martin *et al.*, 1987; Barois, 1987; Syers *et al.*, 1979 for temperate soils).

Earthworm activity creates structures, casts and galleries, which modify the circulation and accumulation of water and gases in soils through changes in the abundance and distribution of pores. This may further affect the decomposition of SOM in the long term (see, e.g. Tisdall and Oades, 1982).

Drilospheric activities may be considerable in terms, for example, of the amounts of soil and organic matter that may annually transit through the guts of endogeic earthworms. On a normally wet year at Lamto (1250 mm rainfall), savanna communities of 2000–4100 individuals ha^{-1} weighing 350–550 kg fresh weight have ingested 800–1250 Mg dry soil ha^{-1} which contained 14–15 Mg organic matter. Figures of several hundred Mg dry soil annually ingested have been indicated for tropical pastures colonized by populations of *Pontoscolex corethrurus* (Fragoso and Lavelle, unpubl. data; Fraile, 1989) and still 100 Mg in arable land in Sweden (Boström, 1988). Such figures are likely to prevail in most humid tropical grasslands where earthworm biomasses of 500 kg fresh weight and absolute maxima of 2000–3000 kg fresh weight have been reported (see, e.g. Barois *et al.*, 1987; Lavelle and Pashanasi, 1989). In tropical forests earthworm communities are generally less abundant and active, with some notable exceptions, e.g. mean

annual biomasses of up to 450 kg fresh weight in south-eastern Mexico (Fragoso and Lavelle, 1987) and peak figures of 900 kg in south-western India (Ferry, unpubl. data).

This review synthesises the results of several years of research aimed at evaluating the short, medium and long-term effects of earthworms on soil organic matter of the humid tropics. Methodologies and detailed results have been published elsewhere (Barois, 1987; Blanchart et al., 1990; Lavelle et al., unpubl. data; Martin, 1992). The significance of these results regarding soil management is discussed and research needs are listed.

SHORT-TERM EFFECTS: NUTRIENT RELEASE IN THE DRILOSPHERE

Assimilation of organic matter

The first, immediate result of the transit of soil through the earthworm gut is the assimilation of a relatively low proportion of soil organic matter (2–6%, e.g. in *Millsonia anomala* with occasional maximum of up to 9%). In experiments using natural ^{13}C labelling *M. anomala* assimilated equal amounts of organic matter from the different particle size fractions (Martin et al., 1991).

When given fresh organic matter, the same worms had contrasted responses. Assimilation was maximum for leaf debris, freshly cut or decomposed for only 2 weeks: growth yield (i.e. growth rate per unit of ingested SOM) was up to twice the control soil value (Lavelle et al., 1989). Legume material with a high N content was especially well assimilated. In contrast, fresh root material was a poor food. After 5–10 weeks of incubation, the quality of organic matter tends to become homogeneous, irrespective of the origin of the material. Soil organic matter which has decomposed for longer periods is assimilated with equal efficiencies, irrespective of the size of particles, normally considered as indicative of their age and their assumed resistance to decomposition.

Comminution may be extremely important: of the 33% decrease of the coarse ($>250\,\mu m$) organic fraction of a savanna soil after transit through the gut of *M. anomala*, ca 5% was due to assimilation and the remaining 28% had been ground into smaller fragments (Martin, 1992). In the gut of the tropical anecic *M. lamtoiana*, assimilation + comminution result in decreases of relative abundance of recognizable fragments of tree-leaves, roots, grasses and seeds by respectively 82.5, 71, 40.5 and 31% (Kanyonyo, 1984).

Nutrient release in casts

Earthworms reject significant amounts of nutrients in their casts. In part these losses result from the intense microbial activity in their gut, and from their own metabolic activity, e.g. elimination of N due to fast turnover of this element in microbial biomass.

Nitrogen

A significant proportion of C assimilated by earthworms is secreted as intestinal and cutaneous mucus with greater C:N ratios than those of the resource used (Lavelle et al., 1983; Cortez and Bouché, 1987). As a result, part of the nitrogen assimilated may be in excess and have to be excreted. Another reason for high mineral-N excretion is the rapid turnover of nitrogen in earthworm biomass as shown by Ferrière and Bouché (1985) for temperate earthworms and further confirmed for the pantropical species *P. corethrurus* (Barois et al., 1987). That nitrogen is mainly excreted as ammonium in the urine released in the gut, in case of species which possess endonephridia. It is thus mixed with the soil and can be found in the casts (Laverack, 1963; Lee, 1985).

In savanna sandy alfisols at Lamto, freshly deposited casts of *M. anomala* contained on average $26.4\,\mu g$ N g^{-1} soil as NH_4^+ and traces of NO_3^- whereas the control soil contained 1.5–$7.5\,\mu g$ N g^{-1} soil as NH_4^+ and no NO_3^-. No significant increase of nitrate concentration was observed during the days following the deposition of casts. It seems as though mineral nitrogen released in fresh casts is readily incorporated into microbial biomass in 8–16 days, when no roots are able to absorb it. Extropolation of these data to the whole drilosphere has been done using the "DRILOTROP" simulation model. Populations of *M. anomala* may annually produce from 5 to 25 kg N ha^{-1} yr^{-1} assimilable nitrogen, depending on year and vegetation types. Production of ammonium was spread all over the year, with a marked increase towards the second half of the rainy season (Fig. 1); in a grass savanna, 82% of this nitrogen has deposited in the upper 10 cm of the soil. 63–71% were released as ammonium in fresh casts, 11–20% as dead worms and the rest as cutaneous mucus and urine.
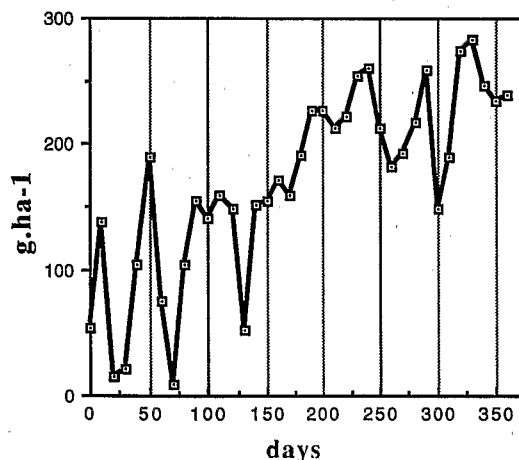

Fig. 1. Ammonium N accumulated in subterranean casts of *M. anomala* deposited 0–8 days ago in a west African savanna (Lamto, Ivory Coast), as calculated by the DRILOTROP simulation model (Martin S. and Lavelle unpubl. data).
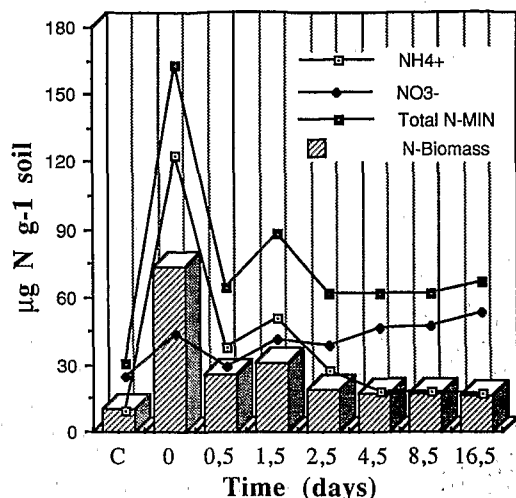
Fig. 2. Changes in mineral-N content and N accumulated in microbial biomass (Nbm) in casts of *P. corethrurus* during the 16 days following deposition (Nbm measured by the Nihydrin method) (Lavelle, Melendez, Schaefer and Pashanasi, unpubl. data).

In forest ultisols, at Yurimaguas (Peruvian Amazonia), mineral-N content in fresh casts of *P. corethrurus* reached 133.1–167.8 μg g^{-1} soil, divided into 106.8 μg g^{-1} soil as NH$_4^+$ and 22.2–46.2 μg g^{-1} soil as NO$_3^-$. In the control soil the corresponding values were 26.1 to 35.8 μg g^{-1} soil total mineral N of which 5.7–6.7 μg g^{-1} soil were in the form of ammonium and 20.0–29.1 μg g^{-1} soil as nitrate. In fresh casts, another 67.5–74.4 μg N g^{-1} soil (10.5–11.3 μg g^{-1} soil in control) were present in microbial biomass (Fig. 2). This stock of labile nitrogen rapidly decreased after deposition of casts: after 12 h the concentration of mineral-N had fallen to 77.7 μg N g^{-1} soil and fluctuated little until day 16.5 when the experiment ceased (Lavelle *et al.*, unpubl. data, Fig. 2).

Ammonium concentration decreased, first sharply, in the first 12 h, then more gently down to a minimum value of 20.6 μg N g^{-1} soil at day 16.5, still more than 3 times greater than the control (6.2 μg N g^{-1} soil). Nitrates had increased by 50% in fresh casts and continued to increase reaching a maximum value at day 16.5 (56 μg N g^{-1} soil). Microbial biomass increased sharply in fresh casts up to 7 times the control value for N-biomass (10.8–71.0 μg N g^{-1} soil) and 2.5 times for C-biomass (48.9–124.8 μg C g^{-1} soil); microbial biomass then sharply decreased in casts at 12 h; at days 1 and 2.5 biomass increased again and finally stabilized at values slightly higher than control for C (+22%), much greater for N (+67%) at the end of the experiment (16 days) (Fig. 2).

These examples illustrate the capacity of endogeic earthworms to trigger a fast mineralization of SOM which results in the release of relatively high amounts of mineral nitrogen in fresh casts.

Phosphorus

Phosphorus availability also seems to be affected by endogeic earthworm activities. An experiment has been done to assess the release of mineral P from a soil with a low P-retention value (ferric acrisol at Lamto, Ivory Coast) and from another with a high value (luvisol at Laguna Verde, Mexico), using a method developed by Fardeau (1981), based on the utilization of radioactive ^{32}P. In casts of *P. corethrurus*, exchangeable and water-extractable inorganic P was more abundant than in non-ingested control soils (Table 1). Fresh (12 h) and aged (96 h) casts obtained from the Lamto soil, contained a higher amount of inorganic exchangeable P than did the control soil. The exchangeable P value of the control soil was fairly low (2.0 μg P g^{-1} soil). In fresh (12 h) casts the concentration had significantly increased (6.0 μg P g^{-1} soil) and increased further in ageing casts up to 15.9 μg P g^{-1} soil after 4 days.

In a comparable experiment performed with the high phosphate sorbing soil of Laguna Verde, water-soluble P and exchangeable P in casts increased after 24 h and further decreased in 4 days casts down to values which did not greatly differ from control and fresh cast soils.

MEDIUM-TERM EFFECTS: PROTECTION IN CASTS

Evolution of organic matter has been observed in medium term (420 days) incubations of casts and a non-ingested control sieved soil (Martin, 1992).

Casts of *M. anomala* were collected 24 h after their production and kept at constant moisture (pF 2.5) and temperature (28°C) for 420 days. At days 0.5, 1, 2, 4, 8, 16, 64, 128, 256 and 420, samples of casts and control soil were taken and analysed. C and N contents were measured in bulk samples and in particle-size fractions isolated from the samples following the method of Feller (1979).

Results showed a clear negative exponential pattern with a rapid decrease of SOM in the early (16) days of the experiment followed by a rapid stabilization and a further blockage of mineralization in

Table 1. Available forms of P (water-extractable and exchangeable) in casts of *P. corethrurus* of different ages from soils with a low (Lamto) and high (Laguna Verde) P retention capacity (Lopez-hernandez, Lavelle and Fardeau unpubl. data) (means accompanied by the same letter are significantly different; $P < 0.05$)

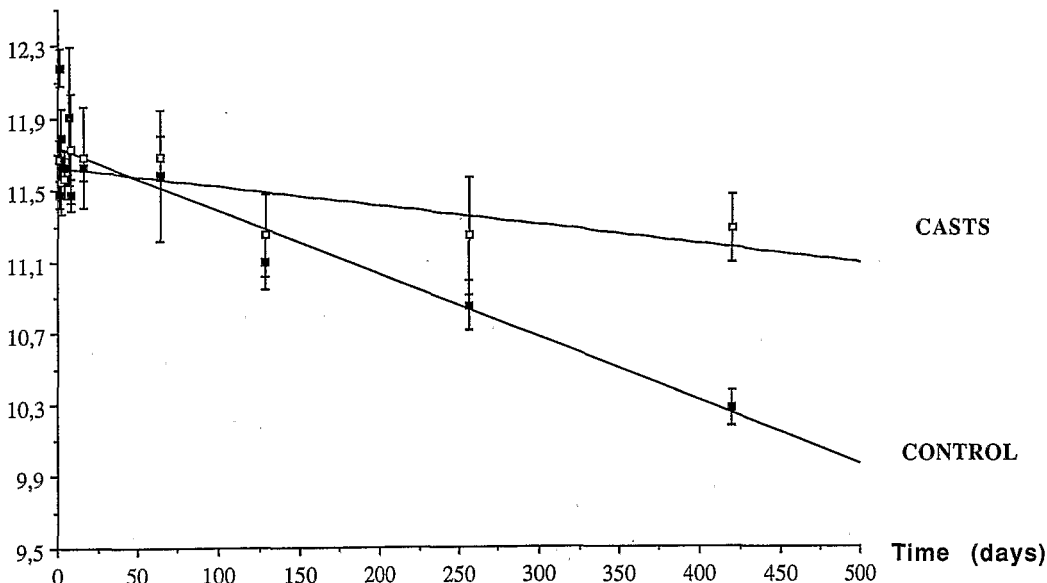|	Water extractable P (μg g^{-1} soil)	Exchangeable P (μg g^{-1} soil)
Lamto (sandy alfisol)		
Control soil	0.060 + 0.005[a]	2.00 + 0.11[a]
Casts 12 h	0.158 + 0.005[ab]	6.00 + 1.78[ab]
Casts 96 h	0.499 + 0.10[ab]	15.89 + 1.78[ab]
Laguna Verde (vertisol)		
Control soil	0.026	15.00 + 0.78[ab]
Casts 12 h	0.021	10.11 + 1.78[ab]
Casts 24 h	0.053	43.33 + 1.11[abc]
Casts 96 h	0.032	11.44 + 1.11[ac]

C Content (mgC/g soil)

Fig. 3. Changes in C of casts of *M. anomala* and a 2 mm sieved control soil during a 420 days incubation (field capacity; 28°C) (from Martin, 1992).

older casts. In the 2 mm-sieved control soil, decomposition was much slower at the beginning, but was further maintained at a much higher rate than in the casts. As a result, the organic content in casts overtook that in control soils, after *ca* 50 days, and was *ca* 10% greater after 420 days (Fig. 3).

Detailed analysis of variations within each particle-size fraction show that, at the scale of this experiment, decomposition of particles larger than 250 μm was decreased by 65% (Fig. 4).

Changes of pore abundance and distribution observed in casts of *M. anomala* as compared to the non-ingested soil are assumed to be responsible for this modified dynamics of SOM. Observation of thin sections of casts of *M. anomala* and non-ingested soil clearly confirm that hypothesis: the casts are more compact than the surrounding soil, and they are enclosed in a thin cover of organic particles and clay minerals. Furthermore, long-term (30 months) field experiments have shown that these structures are
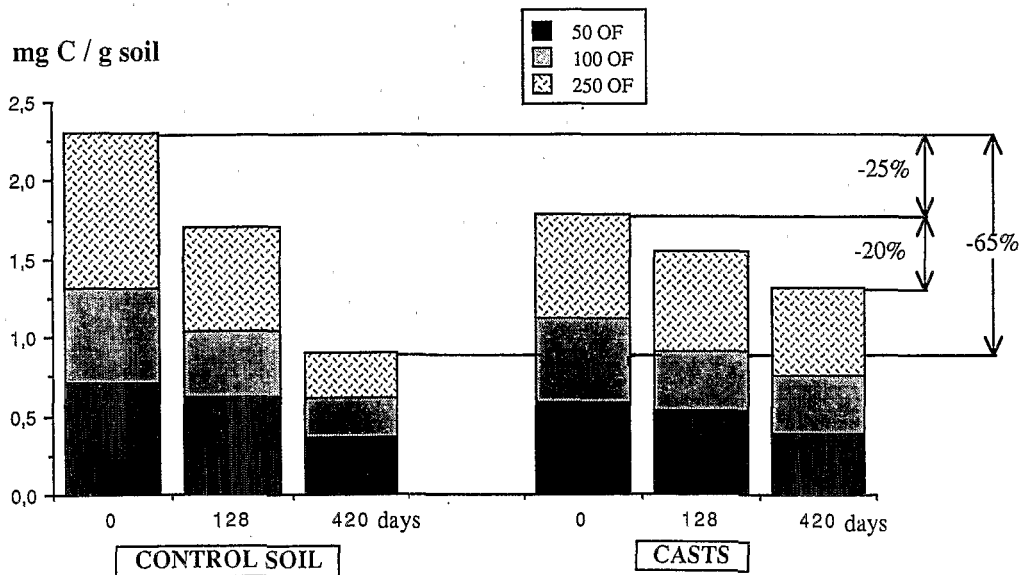
mg C / g soil

Fig. 4. Changes in C-content in the different particle-size fractions of soil organic matter in casts of *M. anomala* and a control soil during a 420 days incubation (field capacity; 28°C). 50 OF = 0–50 μm organic fraction, 100 OF = 50–100 μm organic fraction, 250 OF = 100–250 μm organic fraction.

Table 2. Soil chemical characteristics of two induced savannas from the Mayombe region (Congo), one with, and the other without, introduced earthworms

	Soil layer	C (%)	pH	Assimilable P ($\mu g\ g^{-1}$ soil)	ECEC (meq 100 g^{-1})	S (%)
With earthworms	0–10 cm	1.8	4.72	1.6	2.91	9.2
	10–20 cm	1.7	4.72	1.0	3.60	5.4
	20–30 cm	1.0	4.70	1.3	2.85	1.8
Without earthworms	0–10 cm	2.7	4.68	1.1	4.7	4.0
	10–20 cm	1.3	4.68	0.8	4.28	1.8
	20–30 cm	1.0	4.72	1.0	4.28	1.4

stable in time: in a soil where earthworms had been eliminated, the proportion of large aggregates (>2 mm) remained constant for 2 yr and hardly started to decrease in the upper 2 cm of soil after 30 months. Casts of *M. anomala* thus appear as resistant structures in which SOM may be protected during periods of a few years. Field observations at Lamto indicate that aggregation of soil into aggregates coarser than 2 mm never affects more than 60% of the soil (Blanchart unpubl. data) despite the annual ingestion of up to 60% of soil from the upper 10 cm. This limitation may be due to (1) a limitation of the activity of large earthworms when a large proportion of soil is aggregated into units of coarser than 2 mm because these worms may only ingest aggregates of the size of their mouth, and (2) because small filiform earthworms of the family Eudrilidae may split old casts into smaller ones, 0.5–2 mm. Soil ingestion by the later family may annually represent 120–180 Mg dry soil ha^{-1}.

LONG-TERM EFFECTS: ACCELERATION OF SOM TURNOVER

Long-term effects of earthworms on SOM dynamics in the humid tropics have never been experimentally assessed as in temperate soils (e.g. O'Brien and Stout, 1978; Hoogerkamp *et al.*, 1983) because no comparable long-term experimental introduction of earthworms have been performed so far. In induced savannas of the Mayombe region, comparison of two adjacent soils, with or without introduced populations of *P. corethrurus*, show contrasted compositions. In the plot where no earthworms had been introduced, the soil was compact and humivorous termites were dominant. Although C and N were more abundant in that soil, the grass cover was lower and sparser. In contrast, in the plot where *P. corethrurus* had been accidentally introduced, soil had a well-aerated macroaggregate structure, and was covered by a 1 cm-thick layer of casts. C and N contents of the soil were lower but the grass grew better (Table 2).

At Lamto (Ivory Coast), the turnover of SOM has been assessed in soils with a high earthworm activity, by using the natural ^{13}C labelling of SOM after the shift from a savanna to a forest vegetation. In a savanna which had received only C3 woody material for 16 yr, the proportion of SOM turned over during that time has been estimated at 65% in the upper

10 cm of soil. Significant differences among particle-size fractions were observed: the half turnover time for the coarse fractions (>50 μm) was <1.5 yr whereas that of the fine (<50 μm) fraction was >18 yr. Deeper in the soil, the turnover of SOM was much slower, with a mean mineralization rate close to 40% in 16 yr in the 10–25 cm layer. It is hypothesized that such a rapid turnover of SOM, much greater than values measured so far with similar methods (Cerri *et al.*, 1985; Balesdent *et al.*, 1988) may be due to the intense earthworm activity observed at Lamto.

DISCUSSION

Earthworms affect SOM dynamics of humid tropical soils at four different scales of time and space.

(1) That of the gut transit time which lasts from 20 min to a few hours and, affects a few hundred to >1000 of Mg dry soil $ha^{-1}\ yr^{-1}$.

(2) That of fresh casts (12 h to 4–8 days) which may comprise daily a few Mg dry soil ha^{-1} and last 1–16 days on average.

(3) That of ageing casts, which may comprise a large proportion of the soil, possibly up to 40–60% of the total weight, and represent periods of months to years.

(4) That of the long-term (tens to hundreds of years) evolution of the whole soil profile. The main differences between the effects of humid tropical earthworms and that of temperate earthworm communities are (1) the digestion of humified SOM by the tropical earthworms, when the latter seems to digest only fresh organic debris; and (2) the active aggregation of soils, mainly through casting, by tropical endogeic earthworms, while temperate earthworms only affect the soil physical structure by digging galleries.

Effects of earthworms on SOM dynamics must be investigated at each of these scales to fully understand the process.

(1) At the small scale of a gut transit, the decomposition process is suddenly accelerated with a flush of mineralization and fragmentation of SOM particles into smaller ones. This is a result of the strong priming effect triggered by the addition to soil of water and intestinal mucus, and thorough

mixing which breaks physical protections. Mineralization rates are in the range of a few to 10%, leading to the release of significant amounts of mineral-N (up to 100–130 μg N g^{-1} soil) and assimilable P (maximum values up to 15 μg P g^{-1} soil) in fresh casts.

(2) At the larger scale (i.e. days and hundreds of kg dry soil ha^{-1}) the post-digestive processes operate in the fresh casts: microbial activity continues at a high level for a few days leading to further mineralization, especially of C and P, in the first 24–96 h following cast deposition. After this preliminary stage, re-organization of minerals in microbial biomass or roots, which had been operating since the beginning in the case of mineral-N, becomes a predominant process and soon the microbial activity decreases gradually reaching the original levels. Available data suggest that this return to original conditions would be slower in soils with active clay minerals than in sandy soils.

(3) At the next scale (i.e. years and hundreds of Mg dry soil ha^{-1}) of ageing casts, decomposition processes are dramatically slowed. This would be due to the exhaustion of assimilable substrates and particularly to the physical protection of SOM in the compact structure of casts. This observation which was made with casts of *M. anomala*, of the "round-shaped" category, would probably not apply to "fine granular casts" in which compaction and the resulting faculative anaerobiosis are not important features.

(4) Finally, at the scale of the whole soil profile and decades to centuries, the overall effect of tropical endogeic earthworms has not yet been clearly established. The comparison of two induced savannas in Congo, one with an accidentally introduced population of *P. corethrurus*, the other one without earthworms, would suggest that earthworm activities tend to accelerate the turnover of SOM, a larger part of it being into "active" rather than "passive" forms. This hypothesis clearly needs to be tested.

Endogeic tropical earthworms thus seem to dramatically affect the dynamics of SOM, with different effects depending on the scale under consideration. At the short scale of the gut transit, the mutualistic digestive system with soil microflora induces a considerable acceleration of decomposition and a sudden proliferation of microbial activity. This function largely differs from what has been described so far for epigeic and anecic earthworms. Earthworms of these ecological categories ingest litter or soil supplemented with high proportions of litter. They seem to have an extremely low ability to digest aged soil organic matter (e.g. O'Brien and Stout, 1978; Martin *et al.*,

unpubl. data). They would digest litter, using their own enzymes or enzymes derived from the ingested microflora. They may also partly feed on the ingested microflora (as suggested by Cooke and Luxton, 1980; Cooke, 1983; Rouelle, 1983).

The pattern of nutrient release and microbial reorganization in fresh casts is similar to that observed by Sharpley and Syers (1979) in temperate earthworms. The decrease of ammonium concentration seems to be all the more rapid as temperature and clay activity (related to their abundance and structure) are high. Part of the ammonium is transformed into nitrates or reorganized into microbial biomass.

Ageing casts of the round-shaped category have a key-role in protecting SOM. After 1 yr, casts had a SOM content 11% higher than in a 2-mm sieved control soil, despite the initial decrease due to digestion by the worms. It is expected that different patterns would have been observed with smaller cast units. Field observations and experimentations have shown that large casts are resistant structures. In an experiment where earthworms had been eliminated by flooding, soil macroaggregation only started to become significant after 30 months in the upper 2 cm of soils whereas at greater depth no significant changes had occurred (Blanchart, 1990). It seems that one of the major causes for desaggregation of these casts might be their ingestion by filiform Eudrilidae earthworms and splitting into smaller units. As a matter of fact, large earthworms like *M. anomala* are unable to ingest soil particles larger than the size of their mouth.

The consequences at the level of the whole soil profile of such contrasted effects are still unclear. Two issues seem of particular interest to answer the question, i.e. (1) the possible synchrony of nutrients released through earthworm activities with their uptake by roots. If such a synchrony existed, the drilosphere system would appear as an important source of nutrients for plants; in the opposite case, earthworm activity would only result in a temporary stimulation of the dormant microbial biomass allowing the growth and possible multiplication of cells. (2) Long-term experiments comparing treatments with and without earthworms. Two kinds of situations should be considered, i.e. (i) soils in which earthworms are excluded by, e.g. applications of pesticides, or any other appropriate method (flooding, electricity) which would be less harmful for the environment and (ii) soils without earthworms (e.g. cultivated soils) in which an introduction of adapted species is performed or (iii) cultivated soils with no earthworms which are transformed into pastures or natural fallows and opened to a free colonization by populations from adjacent plots. In such a situation, it would be possible to monitor dynamics of recolonization and subsequent effects on soil parameters. Exclusion of earthworms in small control plot with plastic fabric would help discriminate which are the true effects of their activities.

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