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Review

Effects of tropical endogeic earthworms on soil erosion

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Abstract

Soil biota play a crucial role in influencing soil structure and related soil physical properties. In particular, an abundant literature shows that earthworms, through their burrowing and feeding activities, influence particle size distribution, organic matter content, organic matter location, soil aggregation, aggregate stability and tensile strength, soil roughness, and water infiltration. All those properties greatly influence soil erodibility and soil erosion. Nevertheless, there are few quantitative studies of the influence of earthworms on soil erosion. In some cases, earthworms are said to increase soil losses while other studies emphasize their control on structural stability inducing a reduction in soil erosion. This paper analyses the effects of endogeic earthworms on soil erosion, using recently published data collected in the humid tropics. Endogeics comprise two separate functional groups regarding their effects on soil physical properties, i.e. "compacting" and "decompacting" species whose effects on soil erosion may differ substantially. The effects of these earthworms on soil erodibility and erosion in the tropics ultimately depend on soil types and on the organic matter content in soils. In kaolinitic soils, irrespective of clay content, endogeics greatly influence aggregation, aggregate stability, total porosity and pore size distribution; whereas in smectitic soils (such as vertisols), earthworms have a smaller effect on soil erodibility than soil organic matter and cations. Some options for managing earthworms and organic matter in order to limit soil erosion are also discussed in this paper.

Keywords: Earthworm casts; Soil erodibility; Soil structure; Aggregate stability; Soil porosity

1. Introduction

In the tropics, land clearing and development for food crop production generally lead to chemical, physical and biological degradation of soils. Conserving and/or rehabilitating soil structure and physical properties is much more difficult than maintaining adequate nutrient reserves for plants (Lal, 1994). Controlling soil erosion is therefore essential since erosion imperils the environment and the sustainability of agroecosystems. On a global scale, soil erosion is by far the most widespread cause of soil degradation. Water erosion due to deforestation, overgrazing and agricultural activities affect 1100×10^6 ha in the world (56% of vegetated degraded areas) and among them, 223×10^6 ha are degraded to the point that they are no longer suitable for agricultural land use (World Resources Institute, 1992–1993 in Lal, 1994). The

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reduction or prevention of water erosion is therefore the aim of many soil scientists in order to reduce or prevent particle detachment and transport of the particles in runoff water. A wide range of soil conservation practices have thus been tested and used (conservation tillage, surface mulching, cover crops, terraces, contour tillage, soil amendment with gypsum, etc.) in order to increase surface soil cover, reduce runoff velocity and increase aggregate stability (Roose, 1994).

Information on the role of biological processes on the soil physical condition is important. Nevertheless, the indirect manipulation of these processes through management options to reduce soil erosion is not yet practicable (Papendick, 1994). Earthworms are one of the major groups of soil "invertebrate engineers" that may sustain soil fertility and soil conservation by enhancing the physical, chemical and biological characteristics of soil (Lee and Foster, 1991; Lavelle et al., 1992). In the tropics they are especially abundant in the humid and sub-humid regions.

Studies on the effect of earthworms on soil erosion have been conducted especially in the temperate regions where anecic lumbricid earthworms are dominant. The litter-burying and surface-casting activities of these earthworms can lead to the exposure of soil (previously covered by the surface litter) to raindrop impact and consequent splash erosion (e.g. Hazelhoff et al., 1981; van Hoof, 1983). However, these invertebrates are also responsible for the formation of vertical and semipermanent burrows, which stimulate water infiltration into the soil (Ehlers, 1975; Zachman et al., 1987; Trojan and Linden, 1992; Edwards and Shipitalo, 1998; Shipitalo and Butt, 1999) and reduce surface runoff (Kladivko et al., 1986; Roth and Joschko, 1991). Other studies with endogeic earthworms however, have shown an absence of increased infiltration after inoculation of earthworms (e.g. with *Aporrectodea tuberculata*; Ela et al., 1992). It is well recognized that casts of anecics and endogeics may be easily dispersed and contribute to soil erosion and nutrient losses (Binet and Le Bayon, 1999), especially when they are freshly deposited on the soil surface. In the humid tropics where water erosion represents a dramatic problem due to high rainfall intensity, endogeic geophagous earthworms are dominant (Lavelle, 1983). However, their effects on soil erosion have rarely been assessed or discussed. They are said both to improve the resistance to erosion through an increase in soil infiltration and a higher soil aggregate stability, and also to increase soil erosion through the production of labile casts at the soil surface (Madge, 1969; Lal, 1987; Blanchart et al., 1999).

The main variables that affect soil erosion (splash and surface sealing and crusting) are texture, organic matter, bulk density, water potential, cations, aggregate size and stability and shear strength (Bradford and Huang, 1996; Le Bissonnais, 1996). Numerous studies on tropical earthworm activities have demonstrated that earthworms affect most of these variables through their feeding and burrowing activities. Fig. 1 represents a synthesis of the potential effects of earthworms on soil erosion. Firstly earthworms are able to modify soil roughness by depositing casts at the soil surface. Secondly soil erodibility is directly linked with aggregate stability, which depends on particle size distribution and organic matter content and quality. Earthworms are known to influence these parameters. Though the stability of earthworm casts has been often studied, the results have rarely been related to field behavior and soil erosion. Lastly, earthworms modify

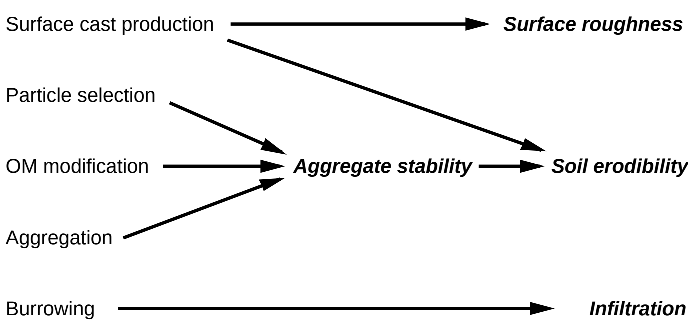

Fig. 1. Potential effects of earthworms on soil erosion.

soil porosity which directly influences water infiltration, hydraulic conductivity and storage capacity in soils.

Some of these mechanisms and their consequences on erosion will be discussed in this paper; and a particular attention will be paid to the relation between earthworms and organic matter in the control of soil erosion. The examples essentially come from studies carried out in the tropics where both kaolinitic and smectitic soils were studied.

2. Earthworm activities and aggregate stability

2.1. Cast production

Cast production can reach very high values and largely depends on earthworm species, as well as their shapes, sizes and casting habits. Lee (1985) and Lal (1987) distinguish two main types of casts: (i) globular casts comprised of coalescent round or flattened subunits with a high stability; (ii) granular casts made of an accumulation of small, fragile, fine-textured pellets. The size of casts depends on earthworm size and ranges from a few mm to a few cm in diameter. In the tropics, surface cast production by endogeic earthworms represents a small proportion of the total volume of egested soil, a most (generally >90%, depending on the species) of which is deposited inside the soil (Lavelle, 1978). The values of surface cast production in tropical regions range from almost nil to 200 Mg ha^{-1} per year (Madge, 1969; Lavelle, 1978; Reddy, 1983; Lavelle et al., 1998; Norgrove and Hauser, 1999a) while the values of total cast production may reach up to 1250 Mg ha^{-1} per year (Blanchart et al., 1999).

2.2. Water stability of earthworm casts

Aggregate stability is one of the main soil properties controlling soil erosion because it is closely related to surface sealing and crusting (Le Bissonnais, 1996). As discussed below, the properties of earthworm casts differ from the bulk soil. Casts are generally enriched in organic matter (OM) and cations, their particle size distribution generally have a higher proportion of the smaller size classes and their density is often higher than soil bulk density. All these properties have important consequences on aggregate stability and erosion (Le Bissonnais, 1996).

2.3. Particle size distribution in casts

Soil texture (and as a consequence the clay percentage) is one of the main soil variables affecting soil surface sealing and infiltration processes (Shainberg and Levy, 1996). Clay particles are particularly important, as the stability of soil structure and aggregates tends to increase with increasing clay content. This is especially due to the aggregation and bonding effect of clay (Le Bissonnais, 1996). Thus, the stability of aggregates against raindrop impact generally increases with an increase in clay content. The influence of soil texture on water stability of aggregates was assessed for temperate earthworm species (reviewed in Tomlin et al., 1995).

Most earthworms selectively ingest mineral and organic particles. The particle size distribution in casts generally has more smaller size classes than bulk soil (Lal, 1987); this is particularly clear for coarse-textured soils and for small earthworm species or individuals (Fig. 2) (Roose, 1976; Barois et al., 1999; Blanchart et al., 1999). For instance, the casts of *Pontoscolex corethrurus*, a medium-sized peregrine species (ca. 1 g when mature) always showed a higher clay content than bulk soil (Barois et al., 1999). This effect was not detected for the adults of *Millsonia*

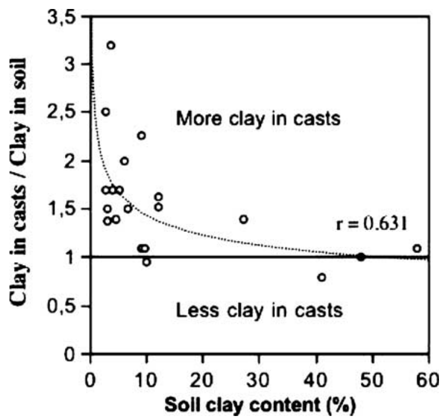

Fig. 2. Effects of clay content on selective ingestion of clay particles by different earthworm species (Barois et al., 1999; reproduced by permission of CAB International).

anomala, a medium-sized species from savannas in Côte d'Ivoire (ca. 5 g when mature); conversely, the casts of young individuals of that species selectively ingest soil particles and there was more clay in casts than in bulk soil (Blanchart, 1990).

The consequences of this selective ingestion and increase in clay content on the stability of casts will be discussed below.

2.4. Organic matter (OM) and cations in earthworm casts

Like the clay percentage, organic matter is a variable affecting soil erosion because it is an important aggregate stabilizing agent in soils. Nevertheless there is an uncertainty on the mechanisms by which soil organic fractions influence aggregate stability and erosion (Le Bissonnais, 1996). Many studies conducted in the tropics showed that most earthworms selectively ingest organic particles, depending on their ecological categories and on the organic content of the bulk soil (Barois et al., 1999). Ecological categories are mainly based on the feeding habits of earthworm species. Epigeics are litter-dwelling and feed on fresh organic materials; anecics ingest a mixture of litter and mineral soil and endogeics ingest bulk soil. Endogeics have different abilities to ingest OM selectively (Lavelle, 1983). Polyhumics feed in microenvironments with higher organic contents, while mesohumics and oligohumics respectively ingest surface soil and deeper horizons, without making a significant selection of organic particles. As a consequence, surface casts of polyhumics are enriched in soil organic matter while those of mesohumics have a same organic matter content as the upper 10 cm of soil. Consequences of these different earthworm behavior in term of soil structure and water stability of casts may be different (Tomlin et al., 1995). The effect of earthworm's diet on cast stability has been mainly studied for temperate species. The greater stability of casts produced by *Lumbricus rubellus* was attributed to more OM incorporation into their casts than those of *L. terrestris* (Shipitalo and Protz, 1988). The analysis of organic matter within earthworm casts, as compared with that of soil, has been rarely studied (Degens, 1997). Guggenberger et al. (1996) showed that the casts of the anecic *Martiodrilus* sp. (Glossoscolecidae) were enriched in carbohydrates and lignin; they concluded that carbohydrate-rich plant debris were responsible for the structural stability of earthworm casts. Same hypotheses were given by Shaw and Pawluk (1986), nevertheless it seems that the location of the organic bonding materials in the soil matrix in more critical than the total amounts (Degens, 1997). Following Degens, the stabilization of aggregates would be due to a physical compression of soil during soil digestion that may enhance the bonding effects of carbohydrate C.

The nature and amount of exchangeable cations influence erosion through their effect on clay dispersion/flocculation processes (Le Bissonnais, 1996). Cations can be classified in the following order, with regard to their effect on aggregate stability: $Ca^{2+} > Mg^{2+} > K^+ > Na^+$. Many studies from the tropics reported an enrichment of exchangeable cations in casts, if compared to the bulk soil (Nijhawan and Kanwar, 1952; Nye, 1955; Roose, 1976; Mba, 1979; Roose, 1980; De Vleeschauwer and Lal, 1981; Lal and De Vleeschauwer, 1982; Mulongoy and Bedoret, 1989; Norgrove and Hauser, 1999b). In this literature, it was mostly observed that the enrichment was more important for Ca^{2+} (three to four times more in casts than in soil) than for other cations (two to three times). In that way, this could explain the better stability of earthworm casts through the enhancement of the complexes of organic colloids with polyvalent cations and clays ("persistent binding agents") (Tisdall and Oades, 1982; Shipitalo and Protz, 1989).

2.5. Porosity in earthworm casts

The density of earthworm casts is often higher than soil bulk density The highest values were reported for the casts of *M. anomala* (endogeics from Lamto's savannas in Côte d'Ivoire); cast density was as high as 1.8–2.0 Mg m^{-3}, whereas bulk density of soil was equal to 1.45 Mg m^{-3} in the upper 10 cm (Blanchart et al., 1993). Moreover, a cortex made of fine organic and mineral particles has been observed for the casts of some species, irrespective of soil texture. The cortex of *M. anomala* was shown to be ca. 25 μm thick and may affect the diffusion of gas and water between the inner and the outer parts of the casts (Blanchart et al., 1993).

Differences in evolution of structure between internal and external parts of casts of *P. corethrurus* during drying have been noted (Duboisset, 1995). Porosity was found to be less important in the external part of casts than in the internal part, irrespective of the age of the cast, and this difference increased with time. The proportion of large pores (as a percentage of soil thin section surface) increased in the internal part of casts (Blanchart et al., 1999). This rearrangement of soil structure could partly explain the stabilization of casts.

2.6. Consequences for water stability of aggregates

All these modifications (particle size distribution, porosity, organic matter content) give specific properties to casts with regard to their water stability and mechanical resistance. Fresh earthworm casts are characterized by a high water content. Although part of the water is reabsorbed in the posterior part of the gut, casts are wet and pasty when egested. Hence, fresh casts often have low water stability, are fragile and may be easily dispersed. With time and drying or drying–rewetting cycles, casts became more water stable (Shipitalo and Protz, 1988). The mechanisms of casts stabilization, i.e. development of fungal hyphae, production of bacterial exopolysaccharides, rearrangement of primary particles (thixotropic changes), addition of intestinal mucus, etc., have been extensively investigated in temperate systems (Marinissen and Dexter, 1990; Zhang and Schrader, 1993; Schrader and Zhang, 1997).

The effect of tropical endogeic earthworms on soil water stability was studied at Lamto (Côte d'Ivoire) (Blanchart, 1992; Blanchart et al., 1997). In one experiment, conducted over 30 months, the development of soil structure (in a 2 mm sieve-fraction) was investigated with and without earthworms (*M. anomala*). Irrespective of the depth (0–2, 2–5, 10–15 cm) and of the test applied (slaking, capillarity wetting procedure, mechanical shaking), aggregates from the treatment with earthworms were significantly more water stable than aggregates collected from the treatment without earthworms (Blanchart, 1992). Thin sections of the top 8 cm of these experimental soils were prepared to investigate the effect of earthworms on soil structure. Strong differences were observed (Fig. 3). The soil with earthworms had a structure characterized by the presence of compact casts. Casts were also deposited at the soil surface where they increased the soil surface roughness; aggregate formation and deposition of casts at the soil surface preventing the formation of a surface crust. Conversely the soil surface of the treatment without earthworms was characterized by the presence of a 2–3 mm thick crust as a consequence of raindrop impact. In another experiment, soil monoliths were defaunated without any modification of initial soil structure, and treatments were established with and without earthworms (*M. anomala*). Soil structure was analyzed after 28 months (Blanchart et al., 1997). Aggregates collected from the upper 5 cm of soil, were less water stable in the treatment with earthworms than those collected from the treatment without earthworms (Table 1). This effect may have been a legacy of old earthworm casts in the soil of the "no earthworm" treatment which were still visible as large aggregates in thin sections. Conversely, in the treatment with earthworms, the soil was constituted by a mixture of old and fresh casts and the water stability was lower than in the treatment without earthworms.

Table 1
Stability (percentage of water stable aggregates, Le Bissonnais method) of 2–5 mm aggregates collected at different depths in three soils submitted to different populations of earthworms after a 28-month period. Mean ± S.D. ($n = 3$) (Blanchart et al., 1997)

Slaking test	Soil depth		
	0–2 cm	2–5 cm	10–15 cm
Earthworm species			
Eudrilid species	32.4 ± 6.1	23.0 ± 1.5	34.5 ± 4.4
M. anomala	20.3 ± 2.8	15.4 ± 2.1	26.0 ± 1.5
No earthworms	66.9 ± 5.0	69.6 ± 3.5	40.6 ± 4.9
Microcracking test			
Eudrilid species	63.4 ± 1.2	65.5 ± 0.4	72.2 ± 3.1
M. anomala	64.7 ± 8.3	64.7 ± 1.7	81.1 ± 6.1
No earthworms	76.2 ± 9.1	82.1 ± 3.3	68.5 ± 3.1
Mechanical shaking			
Eudrilid species	47.8 ± 3.8	39.8 ± 4.0	55.1 ± 3.7
M. anomala	41.8 ± 5.9	40.4 ± 3.5	44.8 ± 1.6
No earthworms	73.9 ± 4.5	66.0 ± 2.5	51.7 ± 3.0

As a conclusion, geophagous earthworms in kaolinitic soils have the ability to increase the percentage of water stable aggregates in soil. This phenomenon has often been measured (review in Blanchart et al., 1999). Recently, a study showed that for kaolinitic soils (Benin, Cameroon), there was a strong negative relationships between the percentage of water stable aggregates larger than 200 μm and soil losses by erosion (Barthès et al., 2000). Thus, by producing water stable meso- and macroaggregates, earthworms could help reduce erosion.

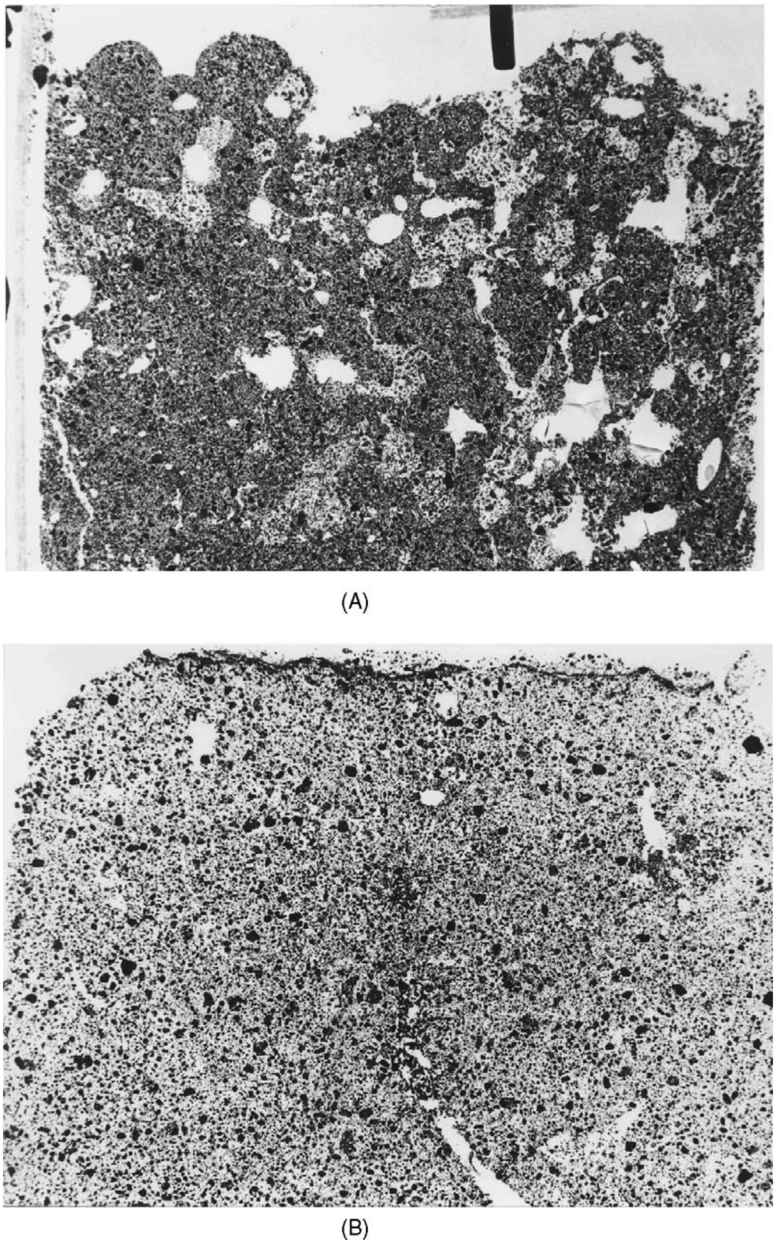

Fig. 3. Thin sections of the 0–8 cm layer of soil after a 30-month period (soil was initially sieved at 2 mm), observed under UV radiation: (A) treatment with *M. anomala*; (B) no earthworm treatment.

3. Earthworm activities and soil erosion in tropical regions

Observations on the disappearance of casts at the soil surface showed that, in wet savannas of Côte d'Ivoire, fresh globular casts of *M. anomala* disappeared after a rainfall event of 18 mm if they were not protected by vegetation cover while those protected by vegetation could persist for many months (Blanchart, 1990). In contrast, granular casts of small eudrilid species (*Stuhlmannia porifera* and *Chuniodrilus zielae*) were easily dispersed and thus contribute to the formation of a surface crust which could impede water infiltration and increase erosion. Actually it seems that the velocity of sealing depends on the moisture content and on the age of casts (Edwards and Shipitalo, 1998; Langhagen, Pfahls, Reelfs, Ries, unpublished data, Sixth International Symposium on Earthworm Ecology, Vigo, Spain, 1998). Similar observations were made for casts of *Martiodrilus carimaguensis* in Colombia (Decaëns et al., 1999a,b; Mariani et al., 1999). The degradation of superficial globular casts was rapid when casts were fresh, and very slow, with a progressive emission of macroaggregates, when casts were dry. The fresh casts dispersed while, after several drying–wetting cycles, dry casts generated a layer of free macroaggregates more stable than the surrounding soil. This layer of stable macroaggregates can protect the soil from particle detachment and crusting by absorbing the kinetic energy of raindrops.

The first observations of a relationship between earthworm cast production and soil losses can be traced back to the end of the 19th century with the publication of Darwin's (1881) book on the formation of vegetable mould. Darwin quoted observations from India, showing that earthworms, in natural situations, were able to influence erosion through the disintegration of surface that washed away to great distance ("and thence in to the plains lying below at a depth of 3000 or 4000 ft", i.e., 900 or 1200 m). Since then, only a few similar studies have been conducted (Nye, 1955; Nooren et al., 1995).

In the early 1970s, Roose (1976) and Roose and Godefroy (1977) investigated the relationships between earthworm cast production and soil erosion. The experiment was set out in the Teke Forest, 40 km north of Abidjan in Côte d'Ivoire (rainfall 1750 mm per year, mean temperature 26.2 °C). The soil was an ultisol developed on Birrimian schist. The production of surface casts by earthworms and soil losses on runoff plots of 100 m^2 were measured over 3 years. The average surface cast production amounted to 50 Mg ha^{-1} per year, whereas soil losses were as low as 0.16 Mg ha^{-1} per year. This study showed that the cast texture was more rich in clay than the neighboring topsoil, but once disaggregated by the splash action of raindrops, the fine particles (clay + loam) were eroded selectively and the remaining material was spread on the topsoil, building a characteristic sandy horizon where the ratio of fine sand/coarse sand was higher than in the deeper horizons (Roose and Godefroy, 1977; Roose, 1980). The recent study of Nooren et al. (1995) confirms the selective erosion of clay in worm casts and the contribution of earthworms to the accumulation of sand on the forest topsoil.

These studies and observations on the effects of earthworms on soil formation and erosion indicate that earthworms may have an important role in the long-term development of soils; but their quantitative roles are still not well understood.

Another experiment was set out in Martinique (West Indies) in order to follow the restoration of soil physical and biological properties when a pasture was installed on a soil degraded by 10 years of intensive cropping and to establish the respective roles of roots and earthworms (*Polypheretima elongata*) in this restoration (Blanchart, 1998; Chevallier et al., 2001). Vertisols developed on volcanic ash in the driest zones are characterized by a high percentage of exchangeable sodium percentage (from 5 to 15%), that make them very sensitive to erosion (Blanchart et al., 2000). The water stability of aggregates which determine the level of soil losses were positively correlated with the soil organic carbon content (Albrecht et al., 1992). These soils were intensively cultivated for market garden crops and pastures. The soil under intensive market garden crops was characterized by low biological activity (earthworms, roots, microbial biomass), low carbon content, weak aggregate stability and high erosion potential. In contrast, the soils under old irrigated and fertilized pastures (*Digitaria decumbens*) had high biological activity, high carbon content, relatively good aggregate stability and relatively low erosion potential. At the beginning of the experiment (i.e. pasture installation), three experimental plots (50 m^2) were installed: (i) no plants, no earthworms; (ii) plants, without earthworms; (iii) plants plus introduced earthworms (*P. elongata*). After 5 years the carbon content in the treatment without earthworms and without plants had significantly decreased if compared to the initial carbon content under market crop (Fig. 4A) (Chevallier et al., 2001). Conversely, in treatments with plants, whether earthworms were added or not, soil carbon content significantly increased after 5 years, but it was still below the C content measured under old pastures. The results were not statistically

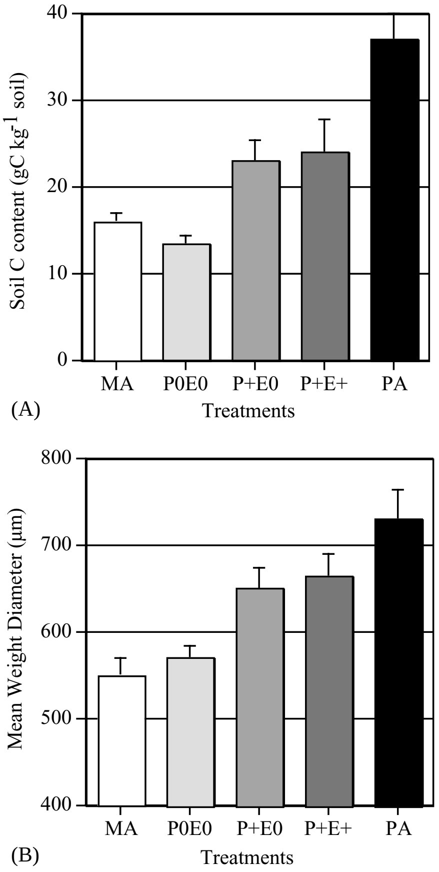

Fig. 4. Effects of plant (*D. decumbens*) and earthworm (*P. elongata*) manipulation on the restoration of (A) soil (0–10 cm) C content ($g\,kg^{-1}$ soil) and (B) aggregate stability (mean weight diameter in the absence of shaking) in a vertisol after installation of a pasture on area previously used for market gardening (measurements taken after a 5-year period). Legend: PA = old pasture, P0E0 = treatment without plants, without earthworms, P + E0 = treatment with plants, without earthworms, P + E+ = treatment with plants, with earthworms, MA = market garden crop (Blanchart et al., unpublished data). Bars indicate standard deviation ($n = 6$).

different in treatment with earthworms versus treatment without earthworms. Water-aggregate stability (Fig. 4B) and structural porosity (specific air volume) measurements (0–10 cm depth) showed results similar to those concerning carbon content: a significant increase in treatments with plants, irrespective of the presence of earthworms. Soil erodibility (turbidity of runoff water and soil losses) was measured, without replication, at the end of the experiment, using a rainfall simulator on a 1 m^2 plot. After 5 years, in the treatment without plants and without earthworms, soil losses were as high as values measured for a degraded soil. Only the two treatments with plants (with and without earthworms) induced a decrease in soil losses, and values tended to be as low as those measured under old pastures. Based on the experiment in Martinique, it seems that endogeic earthworms may have a poor potential to improve aggregate stability and to reduce erosion of smectitic soils (vertisols). In that type of soil, plants in intensive pastures are able to restore soil aggregate stability through high carbon inputs, a stimulation of the microbial activity in the rhizosphere, and water pumping which induces swelling-shrinking phenomena (Cabidoche and Voltz, 1995; Achouak et al., 1999; Blanchart et al., 2000; Cabidoche et al., 2000).

4. Earthworm activities, soil porosity and water infiltration in the tropics

The effects of earthworms on soil structure and especially on soil porosity have been extensively studied in different regions of the tropics. In West Africa, Casenave and Valentin (1988), using rainfall simulation, measured a five-fold higher infiltration if casts were present at the soil surface (10–15 $mm\,h^{-1}$) than if they were absent (2 $mm\,h^{-1}$). Similar results were obtained in Nigeria (Wilkinson, 1975; Lal, 1987). In the Lamto savanna (where the soil has a sand content greater than 85%), many pot and field studies showed that the macroaggregate structure observed in the upper 20 cm of soil was a consequence of intense earthworm activity and especially of the complementary activities of two functional groups of earthworms. Large earthworms (such as *M. anomala*) produced large-sized and compact aggregates whereas small eudrilid earthworms (*S. porifera*, *C. zielae*) produced small, fragile castings. The presence of both groups appeared to be essential to maintain soil structure since experiments showed that the absence of one or the other group resulted in important modifications of soil structure and associated physical properties (Blanchart et al., 1997).

Thus, the presence in the soil of only small earthworms reduced bulk density and the percentage of aggregates larger than 2 mm in a few months. Consequently there was a decrease in water retention capacity and an increase in water infiltration. Similar consequences were observed in situations without any earthworms. Conversely, the presence of large-sized earthworms only induced an increase in bulk density and in the percentage of large aggregates resulting in higher water retention capacity and lower infiltration rates.

These studies allowed the separation of endogeic earthworms into two functional groups with respect to their effects on soil physical properties: compacting and decompacting species (Blanchart et al., 1997; Rossi, 1998; Lavelle et al., 1998). Different experiments (synthesized in Blanchart et al., 1999) confirmed these observations. Experiments with *M. anomala*, at Lamto, showed that this species produced an increase in bulk density (with an increase in macroporosity ~100 μm and microporosity ~1 μm and a decrease in mesoporosity ~10 μm) (Blanchart, 1990; Gilot, 1994; Derouard et al., 1997). The compacting species (*M. anomala*) increased water retention capacity and reduced infiltration rates (22.3 ml min^{-1}) compared with a treatment without earthworms (53 ml min^{-1}) in a pot experiment with maize (Derouard et al., 1997). In Amazonia (Brazil), the intense activity of *P. corethrurus* (also a compacting earthworm species) under pastures produced a compact structure in the upper 10 cm of the soil with severe adverse consequences on water infiltration and soil aeration (Barros et al., 1996; Young et al., 1998; Chauvel et al., 1999). This impermeable horizon was not observed in pastures or forests where soil macro-invertebrate diversity was more important. In Peru, the introduction of *P. corethrurus* into soil induced an increase in the percentage of aggregates >10 mm and a decrease in total porosity (Alegre et al., 1995). With time, in all treatments infiltration rates decreased, but more rapidly so when earthworms were present despite the absence of a surface crust and a better connectivity between macro- and microporosity when both earthworms and residues were present (Duboisset, 1995). Sorptivity (initial infiltration) also decreased in the presence of *P. corethrurus* (Alegre et al., 1995). These authors also observed different soil water regimes depending on earthworm activity. In treatments with *P. corethrurus*, soil was drier in the dry season, and soil was wetter in the rainy season. They hypothetized that the increase in porosity measured in the absence of earthworms had improved water retention capacity.

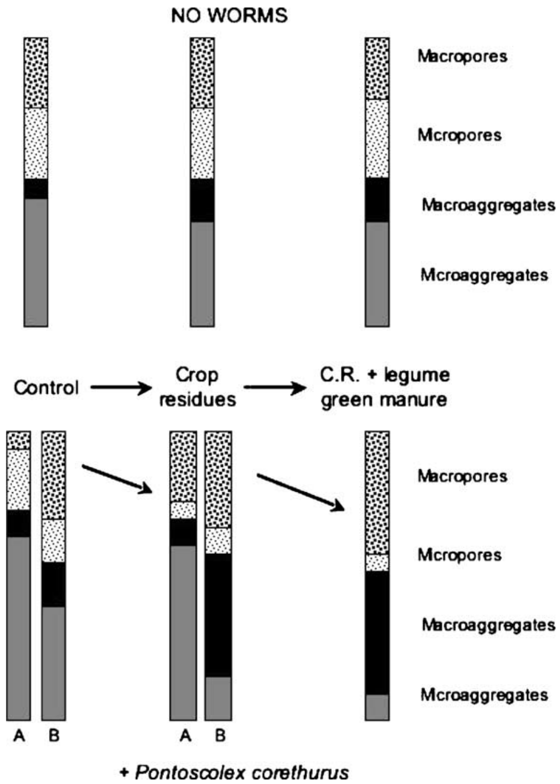

Fig. 5. Effects of earthworm (*P. corethrurus*) introduction and crop residue application on the proportion of aggregates (macro- and microaggregates), porosity (macro- and microporosity) and plant debris in thin sections of soil (0–4 cm) from Yurimaguas (Peru). (A) surface strata (0–1.5 cm), (B) deeper strata (1.5–4 cm) (adapted from Duboisset, 1995; reproduced by permission of CAB International).

In the same sites in Peru, the effects of the introduction of *P. corethrurus* and/or residues on aggregation and porosity were studied by Duboisset (1995) and Hallaire et al. (2000). After 3 years (six crops), thin sections of soil were analyzed and soil structure was described using image analysis (Fig. 5). In treatments without earthworms and without residues, the upper 4 cm of the soil had about 50% porosity and 50% aggregates. The introduction of *P. corethrurus* in the soil induced a strong modification of soil structure in the 0–2 cm depth as well as in the 2–4 cm depth. In the upper 2 cm, compact aggregates became dominant, at the expense of soil porosity and especially of macroporosity, which represented a very low percentage area in the thin sections. This superficial layer became very compact and impermeable due to the coalescence of numerous earthworm casts. Consequently, infiltration was highly reduced in this treatment (Alegre et al., 1995). In treatments with both earthworms and crop residues, macroporosity and macroaggregation were well developed, resulting in relatively high infiltration rates. In this experiment, profiles of porosity, according to the size and shape of pores in the different treatments were analyzed (Hallaire et al., 2000). In treatments with earthworms and without organic inputs, porosity was very small (less than 20% in the upper 2.5 cm of soil) and most pores were small and rounded. In the presence of both earthworms and plant residues, porosity accounted for ca. 30% of the soil and the majority of pores were large and rounded.

The effects of earthworms on porosity and infiltration in vertisols are contradictory. In Martinique, with a humid tropical climate (1300 mm per year), large populations of *P. elongata* are observed under pastures (up to 4 Mg ha^{-1}). Direct observations of earthworm channels showed that these macropores (i) only rarely open at the soil surface and (ii) are generally filled with casts. As a consequence, these macropores may not be efficient for water infiltration, and during high rainfall, these macropores were effectively empty of water (Blanchart, unpublished data). Conversely, in a semi-arid subtropical area of Australia (annual rainfall of 474 mm), earthworm (*Heteroporodrilus mediterreus*) channels are important for maintaining infiltration after the cracks close up. In this experiment, both sorptivity and steady-state infiltration of the soil (under pasture) were strongly affected by earthworm channels which provided preferential flow paths for water (Friend and Chan, 1995).

5. Conclusions

In kaolinitic soils, irrespective of clay content, endogeic earthworms have a high potential for controlling or modifying soil structure and physical properties, and thus in influencing soil erosion (Table 2). “Decompacting” species produce small-sized and labile casts which favor surface sealing and contribute to soil losses. Conversely, they increase soil porosity and water infiltration, which may delay the runoff setting. On the other hand, “compacting” species have the ability to create stable macroaggregates, helping to increase the proportion of water stable macroaggregates in soil, thus decreasing sensitivity to splash effect and runoff. Unfortunately these species by increasing bulk density, induce a decrease in water infiltration. This is particularly obvious in situations where compacting earthworm species develop abundant populations at the expense of a diverse community of soil invertebrates (Chauvel et al., 1999). Consequently the manipulation of earthworms in order to reduce soil erosion in degraded areas should be carried out only in the presence of a high diversity of ecosystem engineers (including both compacting and decompacting species) and with proper management of OM. It is important to consider that decompacting species may belong to other taxa like enchytraeids or millipedes (Lavelle et al., 1998).

In order to understand better the influence of earthworms on soil erosion in the tropics, there is an important need for studies in which earthworms are manipulated for their direct link with soil erosion, and not only for their well-known effects upon infiltration and aggregate formation and stabilization. This need for measuring soil losses in field conditions is mainly

Table 2
Comparative effects of endogeic compacting and decompacting earthworms on soil properties affecting soil erosion

Compacting earthworms (medium- or large-sized worms)	Decompacting earthworms (generally small-sized worms)
Low modification of soil texture	High modification of soil texture
Generally mesohumics or oligohumics	Generally polyhumics
Stable (when dried) globular surface casts	Labile granular surface casts
Limit surface sealing	Facilitate surface sealing
Water stable soil structure	Unknown effect on water stability
Macroaggregation (>2 mm)	Mesoaggregation (0.2–2 mm)
Increase bulk density	Decrease bulk density
Increase water retention capacity (in sandy soils)	Decrease water retention capacity (in sandy soils)
Decrease water infiltration	Increase water infiltration

based on the fact that aggregate stability (as measured by a large variety of tests) and total soil C content are not always directly related to soil erosion.

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