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REGULATION OF SOIL STRUCTURE BY GEOPHAGOUS EARTHWORM ACTIVITIES IN HUMID SAVANNAS OF CÔTE D'IVOIRE

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Summary—The role of endogeic earthworms in the maintenance of the structure of an African savanna soil has been investigated in a 28-month field experiment. Changes of aggregate size distribution, porosity and aggregate stability were analysed in undisturbed soil monoliths from which earthworms had been removed and which had then been submitted to four treatments: (1) recolonization by natural savanna fauna (control, 12 replicates), (2) introduction of a population of *Millsonia anomala*, a large earthworm (13 replicates), (3) introduction of a population of small filiform eudrilid earthworms (13 replicates), and (4) no recolonization by earthworms (12 replicates). At the end of the experiment, significant differences were observed among the four treatments. *M. anomala* was responsible for the formation of macroaggregates > 5.0 mm whereas eudrilid earthworms egested smaller aggregates (0.5–5 mm). The results suggest that the presence of both types of worms is necessary to maintain the natural soil structure. If one or both types of worm are excluded from the soil, the initial structure is greatly affected. © 1997 Elsevier Science Ltd

INTRODUCTION

In humid tropical savannas, endogeic earthworms are always a dominant component of the soil fauna biomass (Lavelle, unpubl. PhD thesis, University of Paris VI, 1978; Lavelle, 1983) and they have considerable effects on the dynamics of the soil structure and soil organic matter (SOM) (Lee, 1985; Lavelle *et al.*, 1992). A research programme has been developed at Lamto (Côte d'Ivoire) to quantify the effect of earthworms on soil properties. Significant effects on SOM dynamics have been described at different scales of time and space (Martin, 1991). Experiments have shown that large specimens of *Millsonia anomala* (Megascolecidae) and small eudrilid worms are able to create a macroaggregate structure from a soil previously sieved (2.0 mm), and that the size of the aggregates produced is proportional to the size of the worms (Blanchart *et al.*, 1989, 1990; Blanchart, 1992). In this paper we address the role of earthworms in the maintenance of the soil structure under field conditions. The earthworm fauna of undisturbed soil monoliths was manipulated in order to produce the following four treatments: (1) natural earthworm community (control), (2) presence of *M. anomala* only, (3) presence of eudrilid worms only, and (4) absence of earthworms. The aggregate size distribution, soil porosity and aggregate stability were measured in the different treatments after 6, 13 and 28 months.

MATERIALS AND METHODS

Study site

This study was conducted between May 1987 and October 1989, in a shrub savanna, at the Station d'Ecologie Tropicale de Lamto (Côte d'Ivoire: 5°02′ W, 6°13′ N, elevation 105 m). The soil is a sandy alfisol (ferruginous tropical soil) with 10% kaolinitic clay minerals, 80% sand (50 μm–2 mm), and low organic matter (ca. 1% C) and cation (3.6 cmol(+) kg^{-1}) contents in the upper 10 cm. In 1986, 1987, 1988 and 1989, mean annual temperatures were 27.9, 28.8, 28.2 and 28.1°C, respectively, and the annual rainfall figures were 973.5, 1100.0, 1450.0 and 1532.3 mm, respectively. Means of both parameters for the last 30 y are 28°C and 1200 mm, respectively.

Earthworms

Earthworms were not abundant in shrub savannas in 1987 (20.2 g fresh weight m^{-2} in October) due to low rainfall conditions. Their biomass was higher in

1988 (42.9 g m^{-2} in May; Blanchart, unpubl. PhD thesis, University of Rennes, 1990). The earthworms used in the experiments were *M. anomala* (Megascolecidae), *Chuniodrilus zielae* and *Stuhlmannia porifera* (Eudrilidae). *M. anomala* is a medium-sized, mesohumic endogeic, geophagous earthworm (17 cm in length and 0.8 cm dia on average at the adult stage) which comprised ca. 23% of the earthworm biomass at Lamto during 1987–1988. Both eudrilid earthworms are small, filiform (3–7 cm in length, 0.5–1 mm dia), polyhumic endogeic species which comprised ca. 91% of earthworm density and ca. 11% of biomass during 1987–1988. The difference between mesohumics and polyhumics is related to the relative organic richness of the soil that they ingest. Polyhumics ingest a soil with a higher organic content than the bulk A1 horizon, i.e. mainly the fine, organic rich, soil particles. Mesohumics ingest the A1 soil without making any selection.

Experimental design

The experiment was conducted in a shrub savanna on a 50 × 50 m plot. Fifty soil monoliths (30 × 30 × 25 cm) were taken from this plot in May 1987, in a period during which the soil was saturated with water and earthworm cocoons were very rare. Earthworms and cocoons were eliminated by immersing the monoliths for 2 d in cold (25°C) water and a further day in warm (40°C) water. This treatment did not significantly affect the soil structure since the monoliths, collected during the rainy season, were already saturated with water before immersion. Vegetation was not affected by this treatment either. The monoliths without worms were placed in stainless steel mesh (50 μm) bags which were open only at the upper part, and then these bags were placed in new holes dug in the shrub savanna. The space between the walls of the monoliths and the holes was filled with soil. Colonization by earthworms crawling at the soil surface was not possible as the lateral edges of the bags were 5 cm above the soil surface.

Four treatments were applied: (1) original earthworm community (control): bags were torn in order to create large openings and allow the recolonization by the nearby soil fauna; (2) Eudrilidae: 15–20 worms were added to each monolith of this treatment (0.75 g fresh weight per monolith, i.e. twice the natural biomass of these species); (3) *M. anomala*: a biomass of 5 g was introduced, i.e., two juveniles each weighing ca. 0.75 g and two sub-adults each weighing ca. 1.75 g-this is equivalent to a biomass of 555 kg ha^{-1}, i.e. twice as much as the peak natural biomass of this species during normally moist years; (4) no earthworms: the absence of casts at the soil surface during the study confirmed the absence of earthworms. Vegetation was allowed to grow, and was burnt each year during the dry season (January) by savanna fires. The experiment started in June 1987 and lasted 28 months.

Analysis of soil physical parameters

Aggregate size distribution was measured using a dry-sieving method specifically elaborated in accordance with local soil properties (Blanchart *et al.*, 1989, 1990). Soil aggregates were separated into 11 size classes-ultrafine: < 0.25, 0.25–0.315, 0.315–0.4, 0.4–0.5; very fine: 0.5–0.63, 0.63–1.0; fine: 1–2; medium: 2–5; coarse: 5–6.3, 6.3–10; and very coarse: > 10.0 mm. The soil monoliths were sampled after 6, 13 and 28 months (three replicates on each sampling occasion). They were separated into five soil strata, i.e. 0–2, 2–5, 5–10, 10–15 and 15–25 cm.

A correspondence analysis with instrumental variables (CAIV, Sabatier *et al.*, 1989; Lebreton *et al.*, 1991) was carried out using the computer programme BIOMECO (Lebreton *et al.*, 1987) to discriminate between the effects of the four treatments, three sampling dates and five soil depths on the aggregate size distribution.

The bulk density of the soil (0–10 and 10–20 cm depths) was measured using PVC cylinders 10 cm high and 5.3 cm dia (volume = 220.6 cm^3). The overall structure and functional volumes such as aggregates, water and pore volume (micropore and macropore spaces) in the upper 10 cm of soil of different treatments were quantified at the end of the experiment (28 months) using the soil shrinkage method (Braudeau, 1988).

Thin sections were obtained from the soil monoliths collected in the upper 12 cm (8 × 8 × 12 cm). Air-dry samples were impregnated with a polyester resin. Addition of a fluorescent dye to the impregnating mixture enabled the observation of pores on soil block surfaces under UV radiation. The terminology used to describe the thin sections is that of Bullock *et al.* (1985). The proportions of different structural units in thin sections were assessed by counting them on a 600 point grid.

Aggregates of the 2–5 mm class from three treatments (*M. anomala*, Eudrilidae, no earthworms) and three depths (0–2, 2–5 and 10–15 cm) were submitted to three stability tests described by Le Bissonnais (1988). In the first test, aggregates were submitted to a slaking, due to air compression by water in pores during wetting. In the second test, aggregates were submitted to microcracking, due to swelling (capillarity wetting procedure). In the third test, aggregates were submitted to a mechanical shaking. Details of the test procedures are described in Blanchart (1992).

RESULTS

Aggregate size distribution

In a natural shrub savanna soil, the size distribution of aggregates changes little with time (Blanchart, unpubl. PhD thesis, 1990). About 37% of the original soil comprises coarse and very coarse aggregates > 5.0 mm, the upper horizon being less

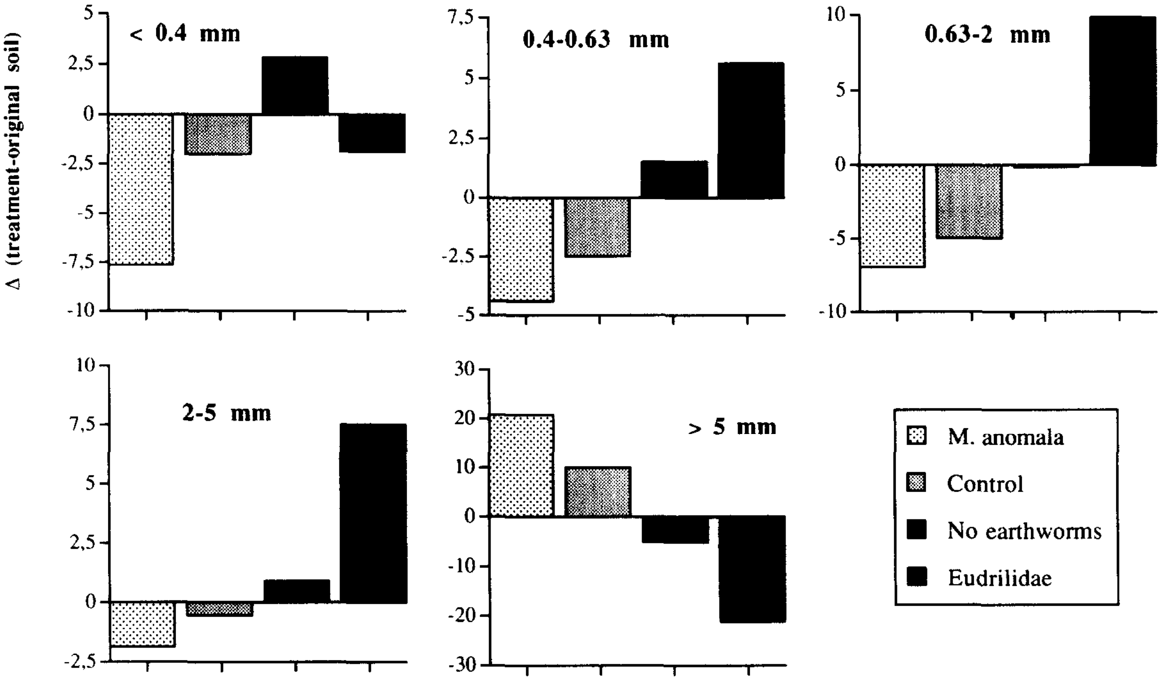

Fig. 1. Percentage difference between soil aggregate size classes in different treatments after 28 months of experiment and soil aggregate size classes in original soil (0–15 cm depth).

macroaggregated (ca. 31%) than the deeper 15–25 cm horizon (ca. 48%) (Blanchart, 1992). At the end of the experiment, the proportion of soil as coarse and very coarse aggregates (> 5.0 mm) in the upper 15 cm greatly differed among the four treatments, with values of 50.5% in the control, 61.3% in the "*M. anomala*" treatment, 35.37% in the "no earthworms" treatment, and 19.4% (15.1% between 5 and 10 cm) in the "Eudrilidae" treatment (Fig. 1). Between 15 and 25 cm, the proportions of soil as macroaggregates > 5.0 mm were almost identical (ca. 45%) in all the treatments at all dates. The instrumental variables accounted for 68% of the total variance: the treatment effect accounted for 33% of the total, time and soil depth effects for 7.5%, interaction of treatment and time effects for 11%, interaction of treatment and depth effects for 6%, and interaction of time and depth effects for 3%. The first axis was mainly represented by the treatment effect and the second axis by both time and treatment effects. The soil depth effect was represented on the third axis. The first axis separated the soil of the "*M. anomala*" treatment, characterized by a dominance of coarse and very coarse aggregates (> 5.0 mm), from that of the "Eudrilidae" treatment, characterized by a dominance of very fine and fine aggregates (0.5–2.0 mm). The interaction between treatment and time effects was pronounced (accounting for 11% of the total inertia). This suggests that the effect of time was not the same in the four treatments. In fact, after 28 months, the soil that underwent the "Eudrilidae" treatment was characterized by relatively high amounts of 0.63–5 mm aggregates, whereas the soils of the "*M. anomala*", "control" and "no earthworms" treatments were characterized by relative high amounts of aggregates > 6.3 and < 0.25 mm, aggregates > 6.3 mm and ultrafine aggregates < 0.4 mm, respectively (Fig. 1).

Table 1. Water contents and porosity of savanna soils submitted to different populations of earthworms after 28 months of experiment as determined using shrinkage curves

	Treatments			
Porosity parameters	*M. anomala*	Control	No earthworms	Eudrilidae
Water contents (cm^3 g^{-1})				
Shrinkage limit	1.69	1.69	1.35	1.03
Air entry microporosity point	4.12	3.92	3.73	6.74
Microporosity saturation point	10.82	11.10	9.02	9.20
Retention capacity	16.28	15.51	13.53	11.34
Maximum saturation point	23.77	25.38	31.41	35.95
Porosity at retention capacity (cm^3 cm^{-3})				
Total porosity	38.23	39.61	44.93	48.02
Structural porosity	17.11	19.36	29.33	34.51
Textural porosity	21.12	20.25	15.60	13.50

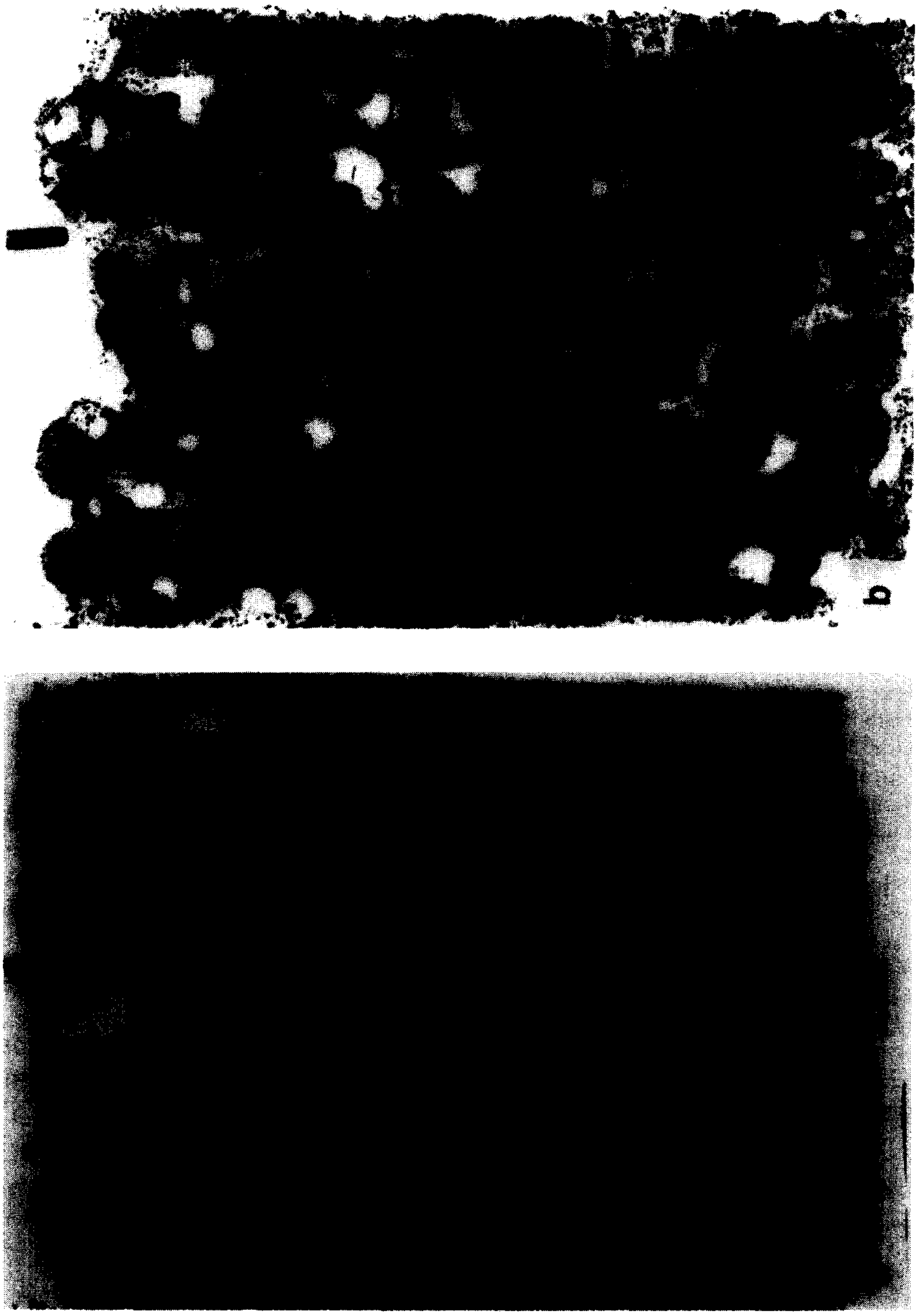

Fig. 2(a,b).

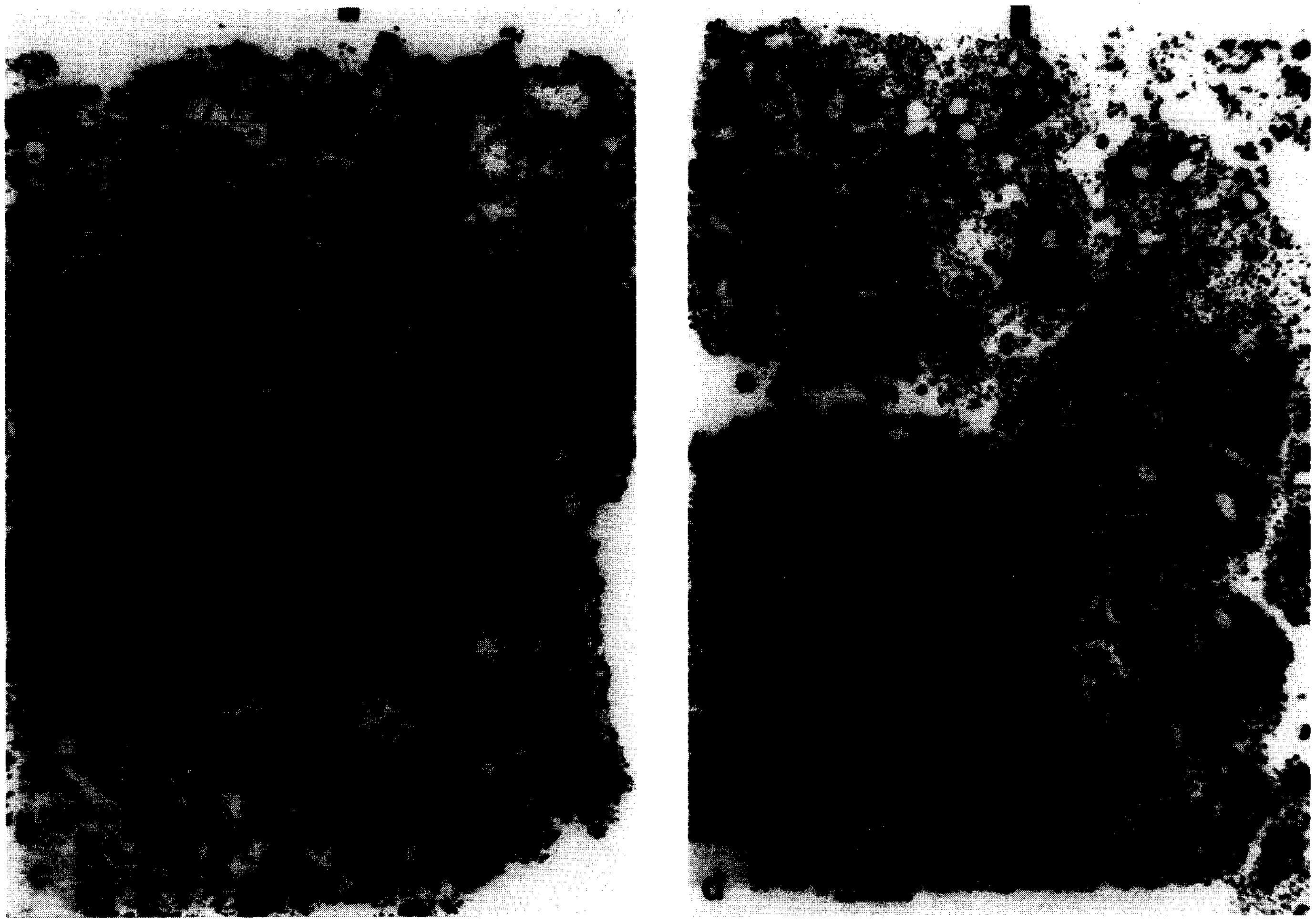

Fig. 2. Thin sections of the 0-12 cm layer of soil after 28 months of experiment, observed under UV radiation: (a) control treatment, (b) "*M. anomala*" treatment, (c) "Eudrilidae" treatment, (d) "no earthworms" treatment. Bar = 1 cm.

Bulk density

After 6 months, the bulk densities were identical (1.22–1.26 g cm^{-3}) in all treatments except for the "*M. anomala*" treatment where it was higher in the upper 10 cm (1.41 g cm^{-3}). After 28 months, differences among treatments were apparent. Bulk densities in the "no earthworms" and "Eudrilidae" treatments had significantly decreased in the upper 10 cm of soil (1.14 and 1.12 g cm^{-3}, respectively), whereas they had increased in the control and in the "*M. anomala*" treatment (1.39 and 1.46 g cm^{-3}, respectively). Shrinkage curve data confirm this trend (Table 1). The upper 10 cm of soil of the "*M. anomala*" and control treatments had comparable shrinkage and pore volume characteristics; they differed from the "Eudrilidae" and "no earthworms" treatments. Other structural characteristics, i.e. the shrinkage limit, air entry microporosity point and microporosity saturation point characteristic of clay-humic fraction, were identical for the "*M. anomala*" and control treatments. In the control treatment, the total porosity at the retention capacity point was equally distributed between structural and textural porosities. In the "*M. anomala*" treatment, textural porosity was greater than structural porosity, whereas in the "no earthworms" treatment, and especially in "Eudrilidae" treatment, the reverse was true.

Micromorphological examination

Thin sections made from the experimental soils after 28 months showed important differences among the treatments. Soils of the "*M. anomala*" [Fig. 2(a)] and "control" [Fig. 2(b)] treatments were characterized by strong compaction due to the presence of numerous large and compact casts, and by the presence of large macropores, which characterize activities of large earthworms (Blanchart, unpubl. PhD thesis, 1990; Blanchart, 1992). The large aggregates were only partly surrounded by voids and thus the pedality was weakly developed. The soil material (aggregates) was only partially surrounded by voids. Aggregates were separated from each other by voids or natural surfaces of weakness. Cast aggregates, voids (chambers and channels) and non-ingested soil represented 73%, 10% and 17% of surface in the "*M. anomala*" treatment, and 75%, 6% and 19% in the control treatment. These soils thus display a typical excremental structure (Fedoroff, *pers. commun.*). In the soils of the "Eudrilidae" [Fig. 2(c)] and "no earthworms" [Fig. 2(d)] treatments, large aggregates corresponding to old casts, at least 28 months old, comprised only 16% of the surface of thin sections in the "no earthworms" treatment and 20% in the "Eudrilidae" treatment, and most of the soil material was included in aggregates < 2.0 mm (76% in the "no earthworms" treatment and 73% in the "Eudrilidae" treatment). Chambers or channels (1–4 mm dia), probably created by ant or termite activities, constituted most of the voids. The main differences between these two treatments were the shape of the old casts and the size of the microaggregates resulting from the disintegration of larger aggregates. In the "no earthworms" treatment, the limits of old casts with the surrounding soil were sharp, since their disaggregation by physical processes along natural surfaces of weakness led to their complete destruction. In the absence of earthworms, aggregates were either completely transformed into ultrafine aggregates (< 0.5 mm) or conserved. In the "Eudrilidae" treatment, the outlines of old casts (rare in the upper 5 cm) were blurred, which indicates that other mechanisms of disaggregation were operating. In that treatment, large aggregates were mainly destroyed by biological rather than physical processes, as they were progressively ingested by Eudrilidae and then excreted as very fine to fine aggregates (0.5–2.0 mm).

Aggregate stability

The slaking test was more destructive than the two other tests, irrespective of the treatments, depth and time after air-drying (Fig. 3). The microcracking test was the least destructive. In the 0–2 cm and 2–5 cm layers, aggregates from the "no earthworms" treatment were more stable than aggregates from other treatments. This was especially true for the slaking and shaking tests. Aggregates from the "Eudrilidae" and "*M. anomala*" treatments had similar stabilities. At a depth of 10–15 cm, differences of stability between treatments were low. Aggregates from the "no earthworms" treatment were less stable at this depth than those at the other depths, whereas the aggregates from the "Eudrilidae" and "*M. anomala*" treatments were more stable at this depth than those at the other depths.

DISCUSSION

After 28 months of exposure to field conditions, aggregate size distribution, porosity and aggregate stability were different among the four treatments. The differences that were still unclear after 13 months became very clear after 28 months.

In the treatment with large earthworms ("*M. anomala*"), the initial biomass (twice as much as the natural biomass) induced a rapid increase in the proportion of coarse aggregates (> 5.0 mm) in the upper 15 cm of soil and a concomitant decrease in soil porosity. This observation confirms similar results obtained by Blanchart (1992). As expected, the soil structure in the control treatment changed little; the main processes responsible for the observed changes were changes in duration of activities of earthworms of different species and physical processes of disaggregation, e.g. water and drying–wetting cycles (Blanchart, unpubl. PhD thesis, 1990). After 28 months, significant changes of the soil structure were

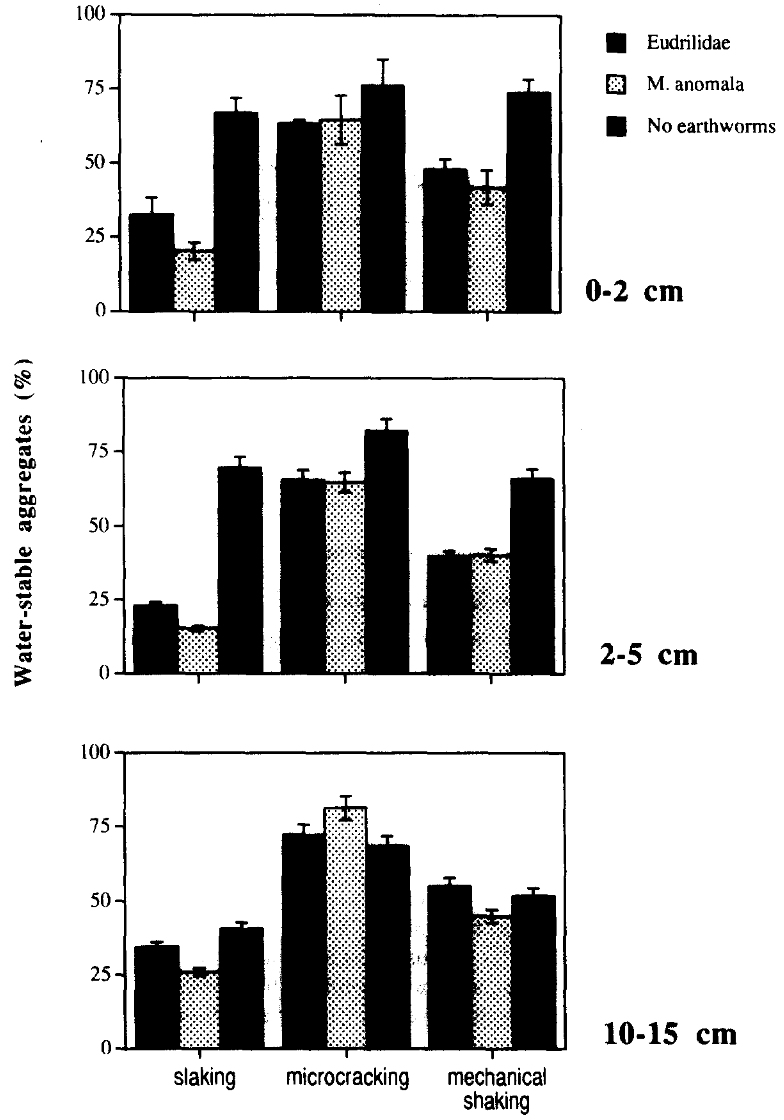

Fig. 3. Stability of 2–5 mm aggregates collected at different depths in three soils submitted to different populations of earthworms after 28 months of experiment. Mean ± SE ($n = 3$).

observed in the "Eudrilidae" and "no earthworms" treatments. Coarse and very coarse aggregates (> 5.0 mm) were destroyed and there was a significant increase in the proportion of intermediate aggregates (0.63–5.0 mm) in the "Eudrilidae" treatment, and of small aggregates (< 0.5 mm) in the "no earthworms" treatment. At the same time, soil porosity, and especially the structural porosity, increased.

Our experiments demonstrated that large *M. anomala* and filiform Eudrilidae have contrasting effects on the structure of the upper 15 cm of the soils at Lamto (Fig. 4). *M. anomala* ingest fine aggregates (< 2.0 mm in diameter) and excrete aggregates larger than 5.0 mm. This species is therefore responsible for the formation of macroaggregates (casts) and large macropores (unfilled segments of galleries, incubation chambers of cocoons and quiescence lodges). The strong compaction of their casts (bulk density of 1.8–2.0) is responsible for the low porosity (Blanchart *et al.*, 1993) in soils where they are abundant. Conversely, eudrilid earthworms mainly excrete casts of a diameter between 0.63 and 5.0 mm, and restrict the formation of large macropores. Furthermore, activities of these small worms significantly decrease the proportions of both ultrafine aggregates < 0.4 mm and coarse and very coarse aggregates > 5.0 mm. Consequently, the small worms favour the destruction of the casts of large worms such as *M. anomala* and thus shorten the mean lifespan of these large aggregates. *M. anomala*, which do not reingest their own fresh casts, also shorten the mean lifespan of casts of Eudrilidae. These two types of worms seem to exert opposite actions on the soil structure (Fig. 4). If one type of worm is excluded, the dynamics of the soil structure is governed by the other type and by the

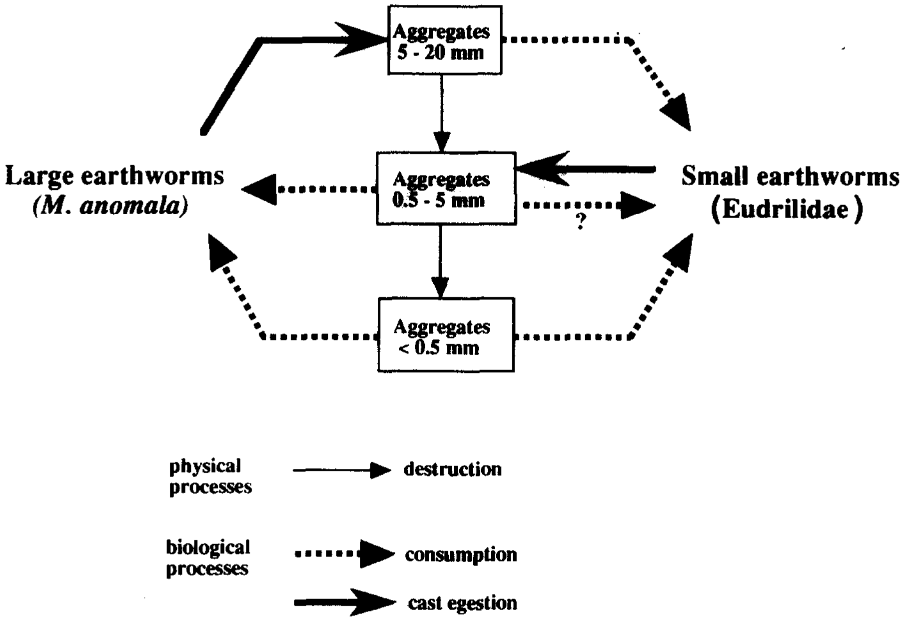

Fig. 4. Conceptual diagram of the complementary roles of large and small earthworms and physical processes in the regulation of the soil structure at Lamto.

physical mechanisms of disaggregation. If eudrilid worms are absent from the soil, large *M. anomala* create large aggregates at the expense of smaller aggregates, and these aggregates > 2.0 mm are then destroyed by physical mechanisms. Blanchart *et al.* (1990) demonstrated that in such a system, and especially when earthworm biomass is high, the soil may be highly compacted. Water infiltration is thus disrupted and environmental conditions are no longer suitable for earthworms. Similar results have been obtained by Rose and Wood (1980) in New-Guinea and by P. Lavelle (1989, *pers. commun.*) in cultivated ultisols from Peruvian Amazonia after inoculation of the mesohumic earthworm *Pontoscolex corethrurus*. When earthworms are excluded (as in the "no earthworms" treatment), the soil structure progressively evolves and a new fine structure slowly appears.

The structural stability of casts increases with time, especially when alternate cycles of moistening and drying occur (Marinissen and Dexter, 1990). In the research carried out here, fresh casts are less stable than the old casts collected in the "no earthworms" treatment. During the dry season, the casts harden and become resistant to disruption by water. In the field, fresh casts mainly produced during the rainy season are resistant to the capillarity wetting procedure, whereas casts hardened during the dry season are resistant to slaking. Fresh casts are less resistant to mechanical processes than are old hardened casts. Resistance to slaking is less at a depth of 2–5 cm than it is between 0 and 2 cm or 10 and 15 cm in earthworm treatments, because the activity of earthworms (both Eudrilidae and *M. anomala*) dominates in this stratum of soil. Conversely, the resistance to slaking is lower in the 10–15 cm stratum than in the 0–5 cm in the "no earthworms" treatment, because the drying and subsequent hardening of aggregates is more important near the soil surface.

CONCLUSION

Large and small filiform endogeic earthworms regulate the structure of the upper 15 cm of the savanna ferruginous soil (alfisol) at Lamto. Large worms are mainly responsible for the formation of the macroaggregate structure by creating aggregates > 5.0 mm and large macropores. In the absence of any factor regulating their effects, the soil is progressively compacted and earthworms die. The mechanisms of this regulation are physical (dependent on rainfall amount and intensity, i.e. water dynamics) and biological, as small earthworms destroy large aggregates and excrete small aggregates. Small eudrilid earthworms actually accelerate the destruction of large aggregates, which are mostly ageing casts of large earthworms, and allow large worms, such as *M. anomala*, to form new large aggregates by ingesting small aggregates.

More research is needed to assess the interactions between earthworms of markedly different size, from different species or within a single species, and of different ages. The relationship between species as hypothesized in this study may provide a clue to understanding the spatial distribution patterns. At Lamto, there is some evidence that Eudrilidae and large Megascolecidae have complementary patchy distributions (Lavelle, unpubl. PhD thesis, 1978). This may indicate that the interaction between the two types of worms is based on a short-term repeating process of the presence and absence of each worm type. The temporal dynamics of their distribution needs to be studied.

The respective contribution of each type of earthworm and of physical factors to the regulation of the soil structure should be quantified, and this study should be extended to soils with different clay contents and mineralogy, and soils where patchy earthworm distributions exist, both in temperate (Poier and Richter, 1992) and tropical areas (Rossi, unpubl., 1992).

Recent experiments have demonstrated that the introduction of monospecific earthworm populations in low-input agricultural systems of the humid tropics may significantly increase crop production during several cropping cycles. Nonetheless, the sustainability of such systems has not been ascertained because soil compaction appears to have negative effects on infiltration, water dynamics and microbial activities (Pashanasi *et al.*, 1992). In this context, the understanding of natural mechanisms regulating the physical structure may help to improve the technique through inoculation of multispecies communities.

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