Soil Biol. Biochem. Vol. 24, No. 12, pp. 1587–1594, 1992
Printed in Great Britain.

0038-0717/92 $5.00 + 0.00

RESTORATION BY EARTHWORMS (MEGASCOLECIDAE) OF THE MACROAGGREGATE STRUCTURE OF A DESTRUCTURED SAVANNA SOIL UNDER FIELD CONDITIONS

ERIC BLANCHART*
Laboratoire d'Écologie, École Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cédex 05, France

Summary—The restoration by earthworms (Megascolecidae) of the structure of a 2.0 mm-sieved tropical ferruginous soil (Ferralsol, FAO) has been studied at Lamto (Côte d'Ivoire).

Soil monoliths (30 × 30 × 25 cm) have been taken in a shrub savanna, 2.0 mm-sieved, homogenized and put back in the field. Then, they have been subjected to three treatments: no fauna (control), original savanna fauna and *Millsonia anomala* Omodeo (Megascolecidae) alone (5 g/bloc).

The distribution of aggregate size classes has been analysed in time (for 30 months) and depth (5 layers from 0 to 25 cm). A micromorphological study using thin sections has been realized, associated with bulk density measurements and 2–5 mm class aggregates have been submitted to stability tests.

The results show an important effect of earthworms in the restoration of original macroaggregated structure by increasing aggregation. In the absence of earthworms, the formation of macroaggregates >2.0 mm is very limited and may be due to dry–wet cycles and microbial activity. After 30 months of experiment, aggregates >2.0 mm only represent 12.9% of soil. Because of a low density due to dry climatic conditions before and during the study, original savanna fauna had not a very important effect during the first year of experiment. Aggregation increased slowly: 12.0% of soil as aggregates >2.0 mm after 14 months of experiment. Then this amount of large aggregates increased more rapidly (49.9% after 30 months). The most important aggregation is realized in treatment with *M. anomala*: 31.7% after 6 months of experiment and 60.6% after 30 months.

The observation of thin sections emphasizes and specifies the role of *M. anomala* in this aggregation. Aggregates created in presence of earthworms are more water-stable than those created in absence of earthworms.

INTRODUCTION

Soils of the humid tropics generally have highly active earthworm communities dominated by endogeic populations. They may ingest annually from several hundreds to 1200 tonnes ha^{-1} dry soil (Lavelle, 1978, 1988). A small fraction (10–50 tonnes ha^{-1}) is deposited at the soil surface as casts which may play a role as factors of soil creeping (when they are fragile) or form a surface mulch which prevents erosion (when they are large and compact). Infiltration of water is always faster when earthworm casts are present (Casenave and Valentin, 1989).

At Lamto (Côte d'Ivoire), a research programme has been developed to evaluate the effects of earthworms on dynamics of soil organic matter (Barois and Lavelle, 1986; Martin A., 1989; Lavelle *et al.*, 1989; Martin *et al.*, 1991) and of soil structure (Blanchart, 1990; Blanchart *et al.*, 1989, 1990). Soils are sandy alfisols with low organic matter (*ca* 1%) and clay (*ca* 7.5% kaolinite) contents. They have, however, an excellent macroaggregate structure which has been attributed to earthworm activities.

This paper reports the results of an experiment which is part of a research programme aimed at assessing the role of earthworms in the formation and maintenance of the macroaggregate structure. In a preliminary short-term experiment, Blanchart *et al.* (1990) have observed the development of structure in 2.0 mm-sieved soil in buckets; 4 treatments were evaluated: control (bare soil), plants alone (*Panicum maximum*), earthworms alone (large species *Millsonia anomala* at different biomasses: 1, 3, 5 g per bucket equivalent to 25, 75 and 125 g m^{-2} respectively), earthworms + plants.

After 2 months, 13.5% of soil had been aggregated as macroaggregates larger than 2.0 mm in the control treatment, and plants had no significant effects (13.8%). Aggregation was rapid and important when earthworms were present (35–59%), irrespective of the presence or absence of plants. The effect was due to the egestion of large compact casts and other mechanisms still unexplained. But this first study presented some disadvantages due to the size of containers and limited duration.

In the present study, formation of aggregates from a 2.0 mm-sieved soil has been monitored under field conditions, with different treatments.

*Present address for correspondence: French Institute, 10 St Louis Street, PB 33, Pondicherry 605 001, India.

MATERIALS AND METHODS

Study site

The study was carried out at the Station d'Écologie Tropicale de Lamto (Côte d'Ivoire). Vegetation is a mosaïc of patches of guinean savannas separated by gallery-forests and forest patches on some plateaus with deep soils. Mean annual rainfall is *ca* 1200 mm and mean temperature, 28°C.

Soils

Soils are poor, tropical ferruginous soils (ferralsols, F.A.O.) derived from a granitic parent material (Riou, 1974). Despite high sand (*ca* 75%) and low clay (*ca* 7.5%) contents, these soils present a strong macroaggregate structure in the upper 15–25 cm. They have a low organic matter content (2% in the upper 10 cm of soil) and low cation concentration (3.2 meq 100 g^{-1}).

Earthworms

Earthworm communities include nine major species with diverse sizes and ecological functions (Lavelle, 1978). The most common species is *Millsonia anomala*, a geophagous, mesohumic endogeic species which represents 40–80% of biomass depending on the type of savanna. These worms reach 17 cm in length and weigh 5 g at the adult stage. In 1972, the population of a shrub savanna had a mean biomass of 211 kg ha^{-1} (*ca* 50% of total earthworm biomass); their soil ingestion was estimated at 500 tonnes ha^{-1} during that year (Lavelle, 1978).

Table 1. Size distribution of aggregate size classes of the original soil of a natural shrub savanna before and after passing through a 2.0 mm sieve

	Total soil (%)			
		Natural savanna soil		
Size of aggregates	Sieved soil	0–2 cm	5–10 cm	15–25 cm
0–250 μ	23.7	13.4 ± 1.3	12.1 ± 2.2	10.6 ± 4.6
250–315 μ	6.7	2.9 ± 0.5	3.0 ± 0.3	2.3 ± 1.0
315–400 μ	18.0	6.8 ± 2.5	7.6 ± 0.5	6.9 ± 2.3
400–500 μ	8.7	5.8 ± 1.2	4.7 ± 1.5	4.1 ± 1.5
500–630 μ	14.0	7.8 ± 4.2	7.1 ± 2.3	5.9 ± 2.0
630 μ–1 mm	16.5	11.3 ± 3.1	9.9 ± 0.6	9.0 ± 2.2
1–2 mm	12.4	9.6 ± 2.9	7.5 ± 1.2	7.4 ± 1.7
2–5 mm	0	9.9 ± 2.7	8.4 ± 1.9	7.6 ± 0.5
5–6.3 mm	0	5.3 ± 1.5	4.2 ± 1.1	3.3 ± 0.4
6.3–10 mm	0	17.1 ± 1.7	18.2 ± 1.7	15.7 ± 1.1
>10 mm	0	10.1 ± 11.7	17.5 ± 10.0	27.2 ± 15.2
<400 μ	48.4	23.2 ± 3.6	22.7 ± 2.9	19.8 ± 7.7
400–2 mm	51.6	34.5 ± 9.6	29.1 ± 5.3	26.4 ± 6.8
>2 mm	0	42.4 ± 9.7	48.2 ± 4.5	53.8 ± 14.4

Experimental design

The experiment was completed in a plot of a shrub savanna measuring 25 × 30 m. One hundred soil monoliths (30 × 30 × 25 cm) were taken from this parcel (only 51 were used for this experiment). They were later air-dried and the soil was destructured and sieved through a 2.0 mm-mesh. Soil was then carefully mixed and put back in the holes where monoliths had been sampled. The size distribution of aggregates of the original and of the 2.0 mm-sieved soil are given in Table 1: aggregates are equally distributed between classes 0.4–2.0 mm (51.6% of total soil) and <0.4 mm (48.4%) for the sieved soil.

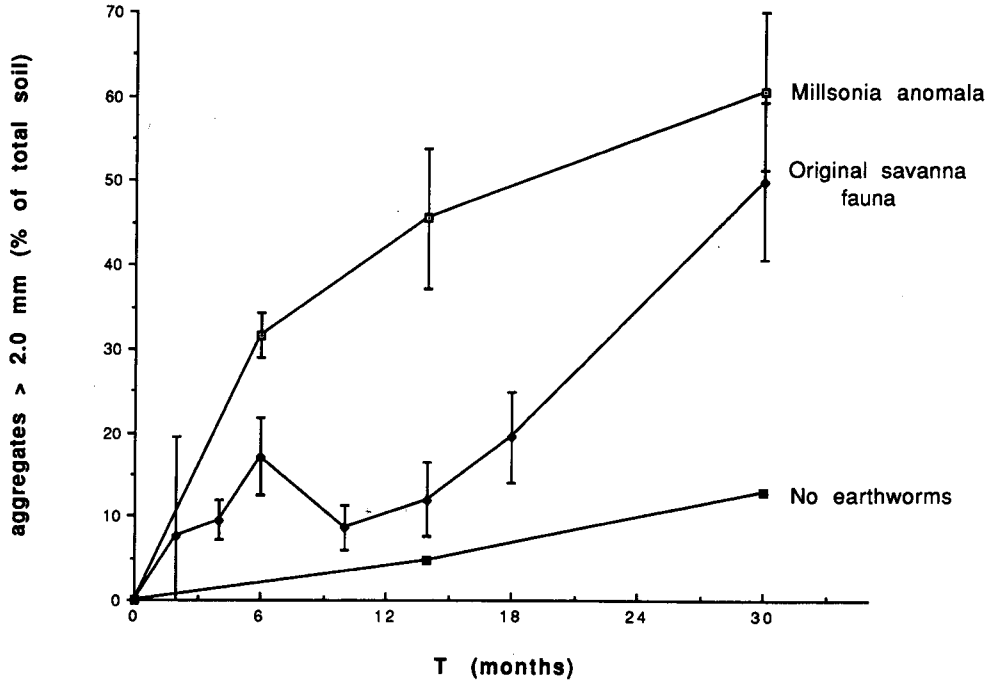

Fig. 1. Evolution in time of the percentages of soil as aggregates >2.0 mm according to various treatments.

Three treatments were applied. To prevent colonization by soil macrofauna, soil monoliths containing known populations of earthworms or no earthworms were placed in nylon 100 μ-mesh bags which were only opened at the upper part. The colonization from the soil surface was not possible as the lateral parts of the bags were 5 cm above the soil surface. Treatments are: (i) no earthworms, (ii) *M. anomala*: a population of 5 g of *M. anomala* (2 juveniles each weighing *ca* 0.75 g and 2 subadults each weighing *ca* 1.75 g) was introduced. This corresponds to a biomass of 555 kg ha^{-1}, i.e. 2 times the natural biomass of this species in normally moist years). (iii) Original savanna fauna: the sieved soil was not separated from the adjacent soil by a mesh bag so that re-colonization by savanna soil fauna was possible.

Fine mesh nets were stretched 5 cm above the soil to limit initial raindrop impact (Roose, 1981). If necessary, these nets were cut to allow the growth of plants and removed after 1 yr. The experiment started in April 1987 and lasted 30 months.

Analyses of the soil structure

Size distribution of aggregates is the main parameter of the soil structure that has been monitored. A dry-sieving method was specifically elaborated in accordance with local soil properties.

The upper parts of plants are cut off; the soil of each monolith (25 × 25 × 25 cm) is then separated into five layers (0–2, 2–5, 5–10, 10–15 and 15–25 cm) each of which are broken into large fragments (*ca* 800 cm^3) and air-dried to a moisture content of *ca* 5–6% dry wt (pF = 4). Aggregates are separated by dropping the air dried fragments from a constant height of 1.5 m onto a hard surface. They are further air-dried and dry-sieved on meshes of the diameter classes listed in Table 1. The separated fractions are weighed and the physical and chemical properties of aggregates thus separated are further assessed. "Original savanna fauna" treatment was sampled at times 2, 4, 6, 10, 14, 18, 30 months (6 replicates) while "*M. anomala*" treatment was only sampled at times 6, 14, 30 months (3 replicates), and "no earthworms" treatment at times 14 and 30 months (only 1 replicate).

Thin sections were prepared at the ORSTOM Laboratory of Adiopodoumé (Côte d'Ivoire), to observe the micromorphological structures created by earthworms in the experiment. They were obtained from soil monoliths collected in the upper 12 cm. The samples were impregnated with a polyester resin. Addition of a fluorescent dye to the impregnating mixture enabled pores to be seen in the thin section surface under ultra-violet (u.v.) light (Fitzpatrick, 1970).

Soil samples collected in PVC cylinder measuring 10 cm height and 5.3 cm dia (volume = 220.6 cm^3) were oven-dried (105°C) to determine the bulk density for different treatments.

Stability tests were used to compare aggregates created by earthworms and other mechanisms in the different treatments of the experiment. We have chosen the tests elaborated by Le Bissonnais (1988) which study elementary mechanisms of aggregate breakdown (slaking, microcracking). Aggregates of the 2–5 mm class have been tested.

(1) First test: slaking resulting from air compression by water inside pores during wetting.

Air-dried aggregates are immersed in water for 5 min. Then water is cautiously evacuated using a pipette and aggregates are immersed in ethanol and 125 μ-sieved. Particles >125 μ are oven-dried (105°C) and dry-sieved at 0.25, 0.5, 1.0 and 2.0 mm without stirring.

(2) Second test: microcracking resulting from swelling (capillarity wetting procedure).

Air dried aggregates are laid on an hydrophilous mesh in contact with water. They are progressively moistened. After 5 min, aggregates are immersed in

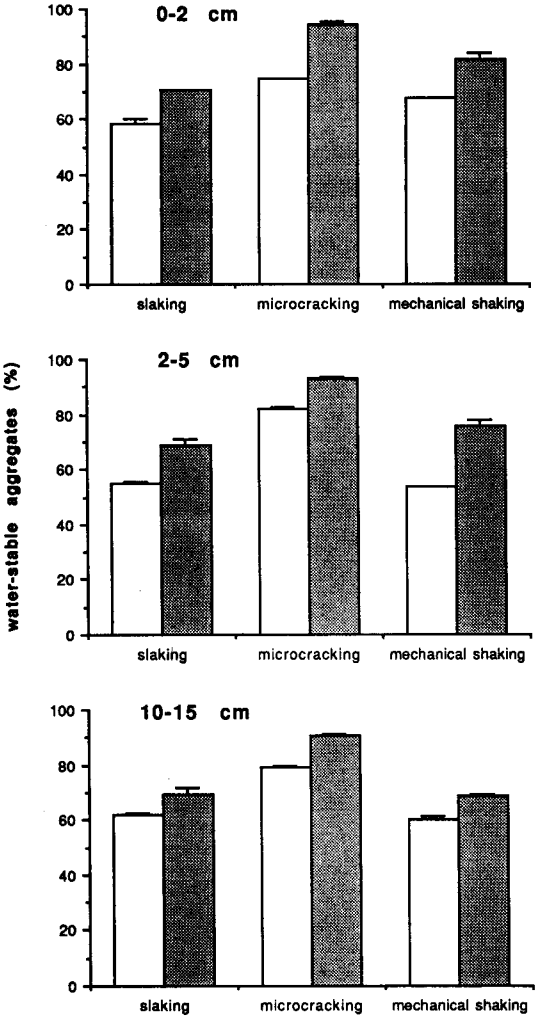

Fig. 2. Water-stability of 2–5 mm aggregates in original savanna fauna treatment (dots) and control treatment (white) at different depths, 30 months after starting of experiment. Means and confidence intervals ($P < 0.05$).

ethanol and 125 μ-sieved. Particles >125 μ are oven-dried (105°C) and dry-sieved at 0.25, 0.5, 1.0 and 2.0 mm without stirring.

(3) Third test: mechanical shaking.

Air-dried aggregates are immersed in ethanol for 5 min. Ethanol is then evacuated and aggregates are immersed in a large quantity of water. The sample is turned over 20 times, let at rest and after 10 min, water is evacuated and aggregates are immersed in ethanol and 125 μ-sieved. Particles >125 μ are oven-dried (105°C) and dry-sieved at 0.25, 0.5, 1.0 and 2.0 mm without stirring.

RESULTS

Time and treatment effects

Structure of the natural savanna soil shows very limited seasonal variations at Lamto (Blanchart, 1990). In the upper 25 cm of soil, *ca* 50% of soil comprise aggregates >2.0 mm and *ca* 20% aggregates <0.40 mm. The upper layer (0–2 cm) is less macroaggregated (42.4% on average of soil as aggregates >2 mm) than the 15–25 cm layer (53.8%) (Table 1). The overall soil bulk density is only slightly lower in the upper 10 cm than between 10 and 20 cm (Table 2).

The size distribution of aggregates observed from the sieved soil (Table 1) differently evolves according to the treatments. The percentages of aggregates >2.0 mm collected in the whole monoliths have been calculated (Fig. 1). In control treatment soil aggregation increases regularly with time (as determined from two samples) and the percentage of soil aggregates >2.0 mm at the end of experiment is 12.9%. At this time, the bulk density is much lower than that of natural soil (Table 2). With 5 g of *M. anomala* per monolith, aggregation increases rapidly and after 6 months of experiment, 31.7% on average of soil is as aggregates >2.0 mm. Then, aggregation continues to increase although a bit slower and at the end of the experiment, 59.9% of the soil has been structured into aggregates >2.0 mm. In this treatment, bulk density increases rapidly in the upper 10 cm of soil (1.40 on average after 6 months) and more slowly between 10 and 20 cm (Table 2). In "original savanna fauna" treatment, the differences between all dates from 2 months to 14 months are not significant due to the dispersion of date (Table 3). We can therefore

Table 2. Bulk density measured in the three treatments and the control soil at different times and depths. Means and confidence intervals ($P < 0.05$)

Treatment (depth)	Date (months after starting) October 1987 (6 months)	June 1988 (14 months)	October 1989 (30 months)
M. anomala			
0–10 cm	1.40 ± 0.06	1.43 ± 0.05	1.43 ± 0.04
10–20 cm	1.23 ± 0.21	1.39 ± 0.03	1.37 ± 0.01
Original fauna			
0–10 cm	1.22 ± 0.07	1.31 ± 0.02	1.32 ± 0.12
10–20 cm	1.26 ± 0.02	1.35 ± 0.07	1.38 ± 0.09
No earthworms			
0–10 cm	ND	1.33 ± 0.04	1.29
10–20 cm	ND	1.32 ± 0.07	1.37
Natural savanna			
0–10 cm	1.42 ± 0.25	1.52 ± 0.04	ND
10–20 cm	1.51 ± 0.09	1.53 ± 0.04	ND

Table 3. Distribution of aggregates (mean values) in three size classes and evolution in time of aggregation in all treatments. Minimal and maximal values are presented in parentheses

Months after starting	Aggregate size classes	Treatments: Original fauna	*M. anomala*	No earthworms
2	>2.0 mm	7.6 (3.5–14.8)	ND	ND
	0.4–2 mm	50.5 (43.9–55.7)	ND	ND
	<0.4 mm	41.9 (39.9–44.4)	ND	ND
4	>2.0 mm	9.5 (7.9–10.2)	ND	ND
	0.4–2 mm	55.3 (54.5–55.6)	ND	ND
	<0.4 mm	35.2 (34.4–36.5)	ND	ND
6	>2.0 mm	17.1 (11.8–25.9)	31.7 (30.5–32.9)	ND
	0.4–2 mm	47.1 (40.2–54.9)	35.4 (34.9–36.3)	ND
	<0.4 mm	35.8 (29.4–40.1)	32.9 (30.7–34.6)	ND
10	>2.0 mm	8.6 (5.2–12.5)	ND	ND
	0.4–2 mm	48.7 (43.8–52.6)	ND	ND
	<0.4 mm	42.7 (40.2–45.3)	ND	ND
14	>2.0 mm	12.0 (8.0–16.5)	45.5 (40.8–49.4)	4.8
	0.4–2 mm	49.2 (45.4–53.4)	31.9 (28.8–36.3)	53.8
	<0.4 mm	38.8 (36.2–41.1)	22.6 (21.9–23.0)	41.4
18	>2.0 mm	19.4 (13.1–27.5)	ND	ND
	0.4–2 mm	47.0 (44.8–48.5)	ND	ND
	<0.4 mm	33.6 (27.7–38.9)	ND	ND
30	>2.0 mm	49.9 (33.2–65.2)	60.6 (56.8–64.8)	12.9
	0.4–2 mm	28.5 (19.7–38.1)	23.0 (20.9–24.8)	45.1
	<0.4 mm	21.5 (15.2–28.7)	16.4 (14.3–18.3)	42.0

Fig. 3. (*See facing page.*) Thin sections of 0–12 cm layer of soils. (a) natural savanna. (b) control treatment after 30 months of experiment (u.v. light). (c) original savanna fauna treatment (6 months). (d) original savanna fauna treatment (30 months) (u.v. light). (e) *M. anomala* treatment (6 months). (f) *M. anomala* treatment (30 months (u.v. light)). Legend: m = *M. anomala* casts; e = Eudrilidae casts; o = casts of other species; v = macropores; t = termite galleries; c = surface crust.

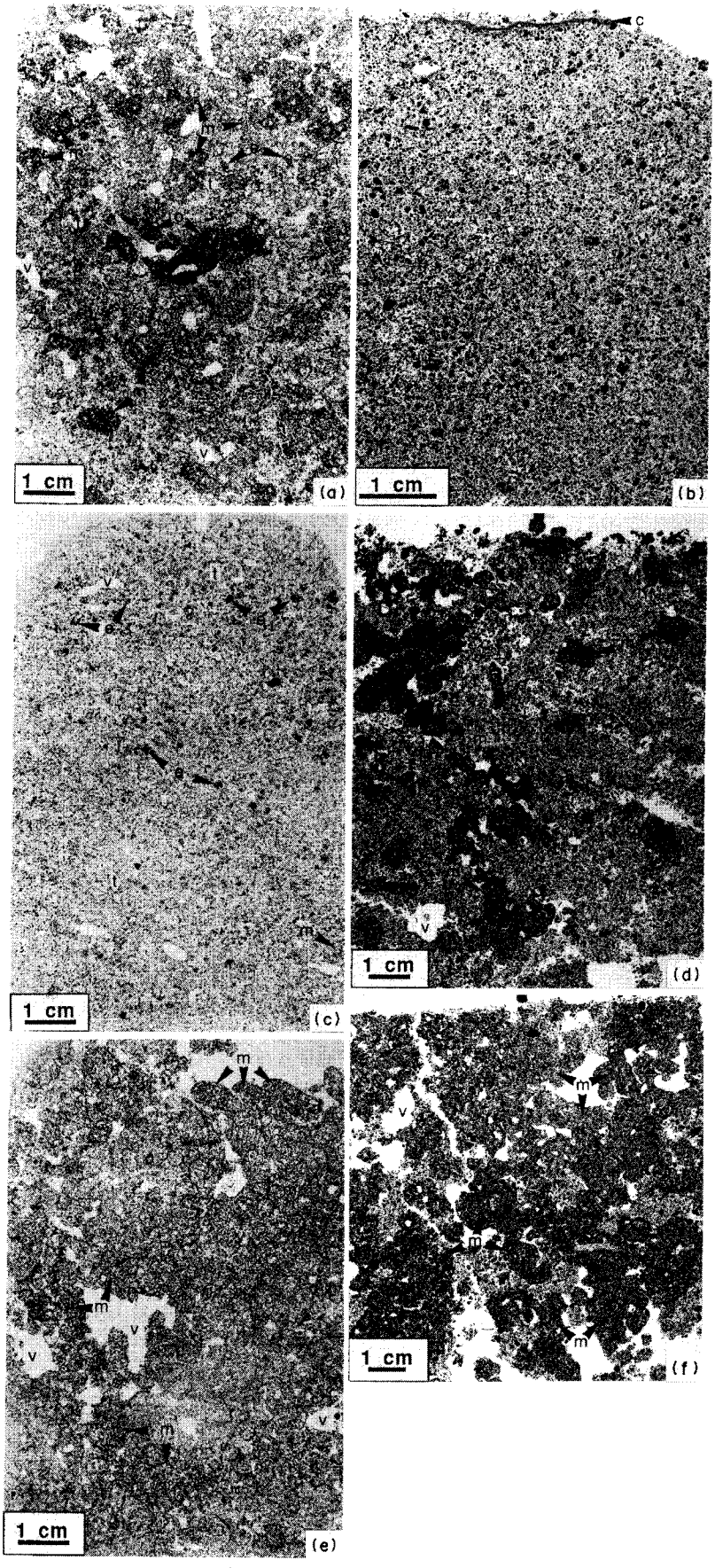

Fig. 3. (*Caption on facing page.*)

infer that aggregation in these soils is slow. Aggregates >2.0 mm only represent around 10% of soil in the first 14 months of the experiment. After 14 months, aggregation increases rapidly and at 30 months, aggregates >2.0 mm represent 49.9% on average of total soil. Bulk density ranges from 1.2 to 1.3 after 6 months of experiment and these values are undoubtedly close to that in control treatment, at the beginning of experiment, if measured. Then, bulk density weakly increases and is hardly lower in the upper 10 cm than between 10 and 20 cm at the end of experiment.

Effect of treatment on aggregate stability

Aggregates in "original savanna fauna" treatment are more water-stable than aggregates in control treatment irrespective of test and depth (Fig. 2). They are more sensitive to the "slaking" test, than to the "mechanical shaking" test and they are more resistant to microcracking due to progressive moistening. The greatest difference between aggregates from "original savanna fauna" and control treatments is observed in the 2–5 cm layer. At 10–15 cm, the difference is lower.

Capillarity wetting procedure induces a low disintegration: 18 (2–5 cm) to 25% (0–2 cm) disintegrated aggregates in control treatments and only 6 (0–2 cm) to 9% (10–15 cm) in "original savanna fauna" treatment. On the opposite, immersion in water is more destructive: 38 (10–15 cm) to 45% (2–5 cm) in no earthworms treatment and 29 (0–2 cm) to 32% (2–5 cm) in original fauna treatment. Mechanical shaking induces an intermediate disintegration: 32 (0–2 cm) to 46% (2–5 cm) without earthworms and 18 (0–2 cm) to 32% (10–15 cm) with earthworms.

Aggregate created in the absence of earthworms are more stable between 0 and 2 cm and between 10 and 15 cm than between 2 and 5 cm; while aggregates formed in the presence of earthworms are more water-stable between 0 and 2 cm. In the latter treatment horizons 2–5 and 10–15 cm give identical results except for mechanical shaking test.

Observations on thin sections

Morphological observations on thin sections show that earthworm casts produced by several species are abundant in the natural soil (Jeanson *et al.*, 1978; Lavelle, 1978) [Fig. 3 (a)]. Two types of casts may be distinguished. The first type (m) is characterized by a dark peripheral layer made of clays and organic matter. These casts which are the most numerous, are fitted in together and fill earthworm burrows. They are certainly recent casts because their structures are not altered: the peripheral layer separates the porous surrounding soil from the compact internal part of the cast where some voids are present between quartz particles. Casts of the second type (o, e) are dark and not outlined by an external layer; they are either casts of other species or ancient casts. "Ageing" characterizing ancient casts makes them hardly recognizable (Bal, 1973). We can therefore infer that at least 50% of the surface in a thin section is occupied by recent or old recognizable casts.

A thin section prepared from the control treatment after 30 months of experiment shows (under u.v. light) an absence of biological structure [Fig. 3 (b)]. The sand particles are uniformly distributed, and the porosity seems to be homogeneous, except two subrounded macropores (t). This soil displays a thin surface crust (c).

After 6 months of experiment, a few macropores (v) due to soil fauna activity are visible in original savanna fauna treatment and the presence of earthworms in soil monoliths is confirmed by a few recent casts (m) [Fig. 3(c)]. On the other hand, small dark aggregates are abundant near the soil surface and are supposed to be casts attributed to small Eudrilidae (e). After 30 months of experiment a thin section of soil of the treatment observed under u.v. light, clearly shows the earthworm casts due to their very low porosity [Fig. 3(d)]. The recent casts are distinct whereas ancient casts more or less disintegrated are not so visible. The surface of thin section occupied by cast was estimated to 32%.

Soils with 5 g of *M. anomala* are much more aggregated after 6 months of experiment [Fig. 3(e)] than soils in original savanna fauna treatment. Large pores have been created by earthworms and recent casts are numerous and present a thin peripheral layer which is characteristic of casts of *M. anomala* (m). Some casts have already lost their characteristic peripheral layer as a result of their ageing. The soil structure has been altered from the beginning of this experiment, due to earthworm activity. This aggregation is even more apparent after 30 months of experiment when the soil is strongly aggregated [Fig. 3(f)]. This thin section observed under u.v. light shows that casts are regularly distributed in the profile. Only some rare soil particles have not been ingested by earthworms. We estimated the surface of thin section occupied by casts to 74%. This structure is characteristic of a "total excremental structure" (Fedoroff, pers. commun.).

DISCUSSION

The dry-sieving method used in our experiment allows separation of aggregates from different origin. Large aggregates (>2.0 mm) may be earthworm casts or aggregates formed by physical (action of soil colloids) or microbial mechanisms (as in the control treatment) (Blanchart *et al.*, 1990). In a sieved soil, *M. anomala* induce a strong aggregation directly dependent on earthworm biomass. This aggregation is more important between 2 and 15 cm depth and never exceeds a limit of 60% of soil as aggregates >2.0 mm.

In treatments and times with low abundance of soil fauna, aggregation at the soil surface may be explained by the formation of a crust due to raindrop

impact, whereas aggregation in depth is mainly due to physical compaction by colloids. In the first stages of original savanna fauna treatment, development of soil structure is low and uneven due to the pattern of colonization by earthworms. This low aggregation may be due both to a low activity of large worms which were not abundant in natural savannas before and in 1987 due to dry climatic conditions (Blanchart, 1990) and a relatively greater activity of Eudrilidae which are little filiform earthworms. These worms have high colonization abilities (Lavelle, 1978) and are able to create a few large aggregates in soil, however, this is much less than large worms (Blanchart *et al.*, 1989).

Rounded-shaped and large-sized casts excreted in the soil seem to be more compact than the surrounding soil and this compaction in the ingested soil in casts induces the creation of large pores (m) between the casts (from 1 mm to 1 cm dia) especially concentrated close to the soil surface [different from termite galleries (t) observed on some thin sections]. In fact, the presence of earthworms causes an increasing of bulk density. This is particularly clear in *M. anomala* treatment as these earthworms essentially act in the first 10 cm of soil; at this depth, bulk density values are the highest. In the original savanna fauna treatment, bulk density is lower in the first 10 cm than between 10 and 20 cm due to the presence of depth species as *Dichogaster terrae-nigrae*. This increasing bulk density, resulting from earthworm activities, seems to be associated with an increasing number of large-sized pores, that confirms the high compaction of soil in casts. These casts are compact even if voids are abundant in them. These voids may be due to 2 mechanisms (Kretzschmar, 1987): reorganization of mineral particles after egestion and retraction of intestinal mucus combined with mineral particles during intestinal transit. The latter explanation is not valid for *M. anomala* because the quantity of mucus in casts is extremely low (Martin *et al.*, 1987).

Another characteristic of the casts of *M. anomala* is the presence of a peripheral layer (cortex) which is *ca* 25 μ thick on average (Blanchart, 1990). It seems to have some hydrophobic properties and probably has some importance for aggregate stability. Aggregates are resistant to microcracking, so soil water has a poor role in cast disintegration, except at the beginning of rain season when slaking may be important. So the life span of cast is all the more long since *M. anomala* do not reingest their own fresh casts (Blanchart, 1990). These worms by creating large aggregates and stabilizing soil organic matter in their casts (Martin A., 1989) have an important effect in the dynamics of soils at Lamto. Dynamics of ageing of these casts, their breakdown into smaller aggregates and their internal porosity need to be investigated in order to better understand dynamics of the soil structure and soil organic matter at Lamto (Lavelle, 1988). This knowledge will be further integrated into the simulation model currently developed (see, e.g. Lavelle and Meyer, 1983; Martin S., 1989).

As a conclusion, our experimental study confirms at a medium time scale results obtained at the lower scale of 2 months (Blanchart *et al.*, 1990). Endogeic earthworms play an important role on soil organic matter dynamics (Martin A., 1989) and on physical soil properties (porosity, infiltration, aeration . . .) at Lamto as the macroaggregate structure observed in the first 15–25 cm results from intense earthworm activity.

Acknowledgements—Financial support for this study has been provided by French "Ministère de l'Environnement" (Sretie) and CNRS (Piren). I am grateful to Professor P. Lavelle and Dr A. Kretzschmar for constructive comments that helped us to improve this paper; to Professor P. Trehen for considerable help, Dr P. Curmi for thin section analysis and Dr Y. Le Bissonnais for stability tests.

REFERENCES

Bal L. (1973) Micromorphological analysis of soils. Lower levels in the organization of organic soil materials. Soil Survey papers No. 6, Soil Survey Institute, Wageningen, The Netherlands.

Barois I. and Lavelle P. (1986) Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biology & Biochemistry* **18,** 539–541.

Blanchart E. (1990) Rôles des vers de terre dans la formation et la conservation de la structure des sols de la savane de Lamto (Côte d'Ivoire). Thèse de doctorat de l'Université de Rennes I.

Blanchart E., Lavelle P. and Spain A. V. (1989) Effects of two species of tropical earthworms (Oligochaeta: Eudrilidae) on the size distribution of aggregates in an African soil. *Revue d'Écologie et de Biologie du Sol* **26,** 417–425.

Blanchart E., Lavelle P. and Spain A. V. (1990) Effects of the biomass and side of *Millsonia anomala* (Oligochaeta: Acanthodrilidae) on particle aggregation in a tropical soil in the presence of *Panicum maximum* (Gramineae). *Biology and Fertility of Soils* **10,** 113–120.

Casenave A. and Valentin C. (1989) *Les états de Surface de la Zone Sahélienne. Influence sur l'Infiltration.* Éditions de l'ORSTOM, Collections Didactiques.

Fitzpatrick E. A. (1970) A technique for the preparation of large thin sections of soils and unconsolidated materials. Micromorphological techniques and applications. Soil Survey Techniques Monographs No. 2, Harpenden.

Jeanson C., Gateau C., Leppert J. M. and Prevosteau J. M. (1978) Quantification à l'analyseur d'images des traces de l'activité des Lombrics et de l'espace poreux disponible pour les micro-arthropodes. Essai de mesure sur une lame mince de grandes dimensions d'un sol ferrugineux tropical (Lamto, Côte d'Ivoire). In *Proceedings of the Fifth International Working Meeting on Soil Micromorphology* (A. Delgato, Ed.), pp. 93–115. Granada.

Kretzschmar A. (1987) Caractérisation microscopique de l'activité des Lombriciens endogés. In *Micromorphologie des sols* (N. Fedoroff, Ed.), pp. 325–330. Association Française pour l'Etude des Sols, Paris.

Lavelle P. (1978) Les Vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème. Publication du Laboratoire de Zoologie de l'École Normale Supérieure, 12.

Lavelle P. (1988) Earthworm activities and the soil system. *Biology and Fertility of Soils* **6,** 237–251.

Lavelle P. and Meyer J. A. (1983) Allez-les-Vers, a simulation model of dynamics and effect on soil of populations of *Millsonia anomala* (Oligochaeta: Megascolecidae). In *New Trends in Soil Biology* (P. Lebrun, H. M. André, A. De Meds, C. Gregoire-Wibo and G. Wauthy, Eds), pp. 503–517. Proceedings of the VIII International Colloquium of Soil Zoology, Louvain-la-Neuve.

Lavelle P., Barois I., Martin A., Zaidi Z. and Schaefer R. (1989) Management of earthworm populations in agro-écosystèmes: a possible way to maintain soil quality? In *Ecology of Arable Land* (M. Clarholm and L. Bergström, Eds), pp. 109–122. Kluwer, Dortrecht.

Le Bissonnais Y. (1988) Comportement d'agrégats terreux soumis à l'action de l'eau, analyse des mécanismes de désagrégation. *Agronomie* **8,** 915–924.

Martin A. (1989) Effet des Vers de terre tropicaux géophages sur la dynamique de la matière organique du sol dans les savanes humides. Thèse de Doctorat de l'Université Paris–Orsay.

Martin A., Cortez J., Barois I. and Lavelle P. (1987) Les mucus de Ver de terre: moteur de leurs interactions avec la microflore. *Revue d'Écologie et de Biologie du Sol* **24,** 549–558.

Martin A., Mariotti A., Balesdent J. and Lavelle P. (1991) Estimate of soil organic matter assimilation of a geophagous tropical earthworm based on ^{13}C natural abundance. *Ecology* **73,** 118–128.

Martin S. (1989) Modélisation de la dynamique des populations de Vers de terre géophages de la savane de Lamto (Côte d'Ivoire): le modèle SOLTROP. In Séminaires SEMINFOR 2: la modélisation: aspects pratiques et méthodologie, pp. 245–262. Montpellier, 26–28 September 1988. Editions de l'ORSTOM. Collections Colloques et Séminaires, Paris.

Riou G. (1974) Les sols de la savane de Lamto. In *Analyse d'un Ecosystème Tropical Humide: la Savane de Lamto (Côte d'Ivoire). I. Les Facteurs Physiques du Milieu.* Numéro Spécial Lamto I, pp. 3–38. Publication du Laboratoire de Zoologie de l'École Normale Supérieure.

Roose E. (1981) Dynamique actuelle des sols ferrallitiques et ferrugineux tropicaux d'Afrique Occidentale. Travaux et Documents de l'Orstom No. 130.