



## EARTHWORMS, WATER INFILTRATION AND SOIL STABILITY: SOME NEW ASSESSMENTS

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**Summary**—Water infiltration (by limiting surface water run-off) and stable crumb formation (by increasing top infiltration and decreasing slaking) are two key soil factors greatly affected by earthworms. Because of the great number of environmental variables controlling (1) earthworm populations; (2) their physical rôle behaviour; (3) their feeding behaviour inducing faeces composition; and (4) the microbial activity stabilizing faeces to crumbs, we chose to make most measurements directly *in situ* in various soils.

The amount of infiltrated water was measured in various soils ( $n = 17$ ) and gave a mean rate of  $150 \text{ mm h}^{-1}$  per  $100 \text{ g m}^{-2}$  of earthworms ( $P < 0.05$ ) and more closely ( $n = 11$ ) or  $282 \text{ mm h}^{-1}$  per  $100 \text{ g m}^{-2}$  of anecic species ( $P < 0.01$ ). A precise study was made in nine sites analyzing hydraulic (= active) burrows and their structural properties. Infiltration rate was correlated to earthworm biomass ( $r = 0.975$ ), burrow length, surface and volume ( $r = 0.99$ ), but not with burrow diameter, tortuosity or with earthworm number and soil profile depth.

Faecal production was also estimated in two fractions: the above-ground casts and the in soil cast fractions. The above-ground production is influenced by seasonal factors (moisture, temperature, photoperiod) and by controlled food types added on soil (natural herbs, wheat straw, lucerne and evergreen oak leaves). The total earthworm faeces produced in the natural food treatment was  $293.6 \text{ kg year}^{-1} \pm 10\%$ , per  $100 \text{ g m}^{-2}$  of earthworms. The amount varied with the food type added to soil. The above-ground fraction is rather small (8% of the total). The stabilization of faeces in crumbs was studied during 536 days by incubation *in situ* (top soil to a 15 cm depth) and in laboratory microcosms, versus the various food types. The crumb stability increased three-to four-fold during a year. The stability in the field depended mainly on the organic food and less on the soil level. The mean turn over rate in the field of earthworm crumbs was 2.3 year. The significance of microcosm studies is discussed and depends on the homeostasy and adaptive behaviour of earthworms (heterochresty). Microcosm results were validated for metabolism and unvalidated for soil bioturbation. © 1997 Elsevier Science Ltd

## INTRODUCTION

The main direct physical rôle of earthworms in soil is an ingestion process followed by digestion and defecation. In addition, earthworms press soil elements together to form burrows and drag elements to their burrows by manducation and body friction (Bouché and Vannier, *in litt.*). These ingestion processes and pressure open burrows, which play a great rôle in fluid movement and other soil life.

Faeces evolve into soil as crumbs, that are more or less stable, to create a typical granular soil structure. Together, crumbs and burrows, increase water infiltration and soil stability and, thus, reduce water run-off and soil erosion. Our work follows a large series of field and laboratory observations made by Darwin (Darwin, 1837, 1881), and Hensen (1877). In this literature estimates of these processes vary widely and include hypotheses as, for example, in the estimation of the annual total production of earthworm faeces. This work is devoted, especially, to measuring, as accurately as possible, the earthworm's soil physical functions in the field. In ad-

dition some laboratory microcosm estimates are compared to field measurements to validate these models.

## MATERIALS AND METHODS

To reduce hypothesis and bias we selected, when possible, direct field measurements to assess (1) earthworm population numbers; (2) burrow network properties; (3) water infiltration; (4) faecal production; (5) faecal stabilization of crumbs. We studied 17 sites, with a large variety of soil types, earthworm species and four ecological categories, for community structure and water percolation. Among them, burrow networks of 11 sites were studied more closely. In these sites, in a dry grassland on a fersialitic calcareous soil, the dominant earthworm species was *Scherotheca gigas mifuga*, Bouché, 1972. This anecic species was used in both field and laboratory microcosms. Full data are presented in Al-Addan (1992). All data are stored in

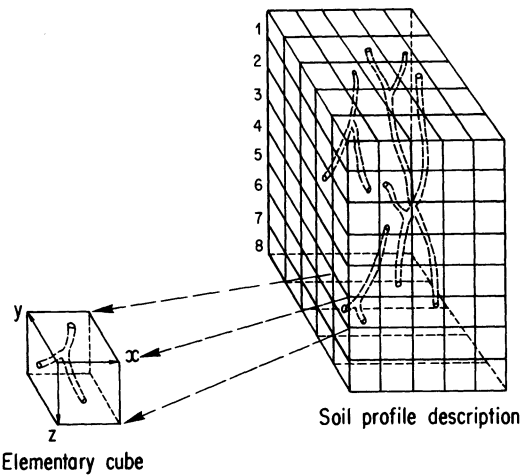


Fig. 1. Active (dyed) burrows are described in reference to a succession of elementary cubes located in the soil profile.

the Relational Data Base BASECOL of ECORDRE (Soto and Bouché, 1993).

1. Earthworm populations were estimated by the ethophysic technique (Bouché and Beugnot, 1972; Bouché and Gardner, 1984). This technique gives two values; one of them, formalin sampling, gives the possibility to estimate the field activity as a ratio related to a total estimate (formalin + washing-sieving techniques) (Bouché, 1975).
2. The burrow network is described only for water infiltration effects. Burrows were dyed by wetting the top soil with a methylene blue water solution. Twelve hours later burrows were described by taking a succession of  $10 \times 10 \times 10$  cm elementary cubes dissected with the help of catheters, introduced to follow the continuity and identity of burrow portions (Fig. 1). With the catheter we measured the true length ( $L_{ie}$ ) and the total length  $L_g = \sum_{i=1}^n L_{ie}$ .

By the observation of hole limits at each side of cubes, we estimated the direct length  $L_{gd}$  where the total is

$$L_{gd} = \sum_{i=1}^n \sqrt{(x_{i+1} - x_1)^2 + (y_{i+1} - y_i)^2 + (z_{i+1} + z_i)^2}$$

The volume is

$$V_o = \sum_{i=1}^n V_i,$$

where  $V_i = L_{ie} \times D_{mi}^2 \times \Pi/4$ , where  $mi$  is the mean dia between the entry and exit dia of the burrow in each block.

Tortuosity, which is important for hydraulic conductivity (Assad, 1987), is expressed as  $Tor\% = (L_g - L_{gd})100/L_{gd}$  Mean diameter is

$$D_{mg} = \sqrt{V_g/L_g}$$

$$\text{inner surface } S_p = \sum_{i=1}^n (L_{ie} \times D_{mi} \times \Pi)$$

3. Mean burrow distance between burrows is

$$D_s = \sqrt{V_s/L_g},$$

where  $V_s$  is the soil volume and  $L_g$  the burrow length in this volume.

Total burrow section is the sum of horizontal burrow surface:

$$S_{ct} = \sqrt{D_{mi}} \times \Pi/4$$

4. Water percolation (infiltration in saturated soil) was measured following the Muntz *et al.* (1905) double ring method. This measurement is made in the inner ring (dia = 50 cm) protected by an external ring (dia = 100 cm) for side effects. The two surfaces, limited by the two rings are kept by a Mariotte vessel under 1–3 cm of water depending on soil irregularities (Fig. 2). Speed of percolation was observed after the initial moistening, i.e. when the infiltration rate was regular.
5. Earthworm defecation was measured by a new technique resulting in the addition of three successive methods. The Lavelle method was to eliminate by crushing all previous crumbs equal or greater than the studied size (here 2 mm dia) allowing us to estimate faecal production (= new crumbs) in microcosm studies (Lavelle, 1971). The Al-Addan method is to make this manipulation under field conditions (field microcosms) and to restore the soil bulk density for each soil layer. Finally the Bouché method to validate the Al-Addan field microcosm estimates by comparison of surface cast productions between field-microcosms and a nearby undisturbed field. This LAB (Lavelle–Al-Addan–Bouché) technique was applied in the field using fibro-cement tubes (dia = 30 cm) buried 30 cm in soil and 5 cm above the soil and filled layer after

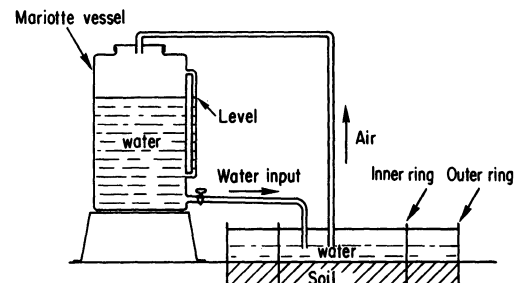


Fig. 2. Settings to measure in field infiltration rate with the Muntz *et al.* double ring method and a Mariotte's vessel.

Table 1. Soil characteristics observed in field and applied to field-microcosms

Soil level	Field density (kg m <sup>-3</sup> )	pF 3 soil moisture (%)
(0-5 cm)	1.1	25.3
(5-15 cm)	1.1	19.4
(15-30 cm)	1.3	19.0

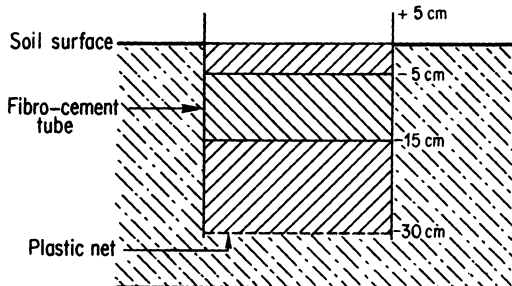


Fig. 3. The field microcosm used to measure faeces production (= crumb formation rate) by the LAB technique.

layer with destructured soil, then compacted to restore the bulk density of each layer (layer -30 to -15 cm, then -15 to -5 cm and -5 to 0 cm) (Table 1). This restores the soil thermoprofile and, to some extent, the moisture profile (Fig. 3). The *in situ* validation of this model was made by comparison with litter-plots having no soil perturbation and with the same litter as in LAB field microcosms (Fig. 4). Earthworms were then rein-

troduced at a similar biomass level as the field (Table 2).

- The litter-plots are made for five purposes: (i) to measure earthworm activity for surface casting; (ii) to measure natural earthworm population changes under various manipulated litters; (iii) to measure percolation rates and (iv) burrow network variables, after litter treatment; and (v) to collect fresh faeces (3.5 days old) which were air dried and accumulated and used later in the crumb incubation experiment.

In these plots, soil was not perturbed or trampled, but the vegetation and top soil litter were eliminated by an initial cut and a hand-weeding. Anecic species, with *Scherotheca gigas mifuga* (66.9% of the biomass) and *S. monspessulensis monspessulensis*, Bouché, 1972 (32.3%) were almost pure in the community with only a few of the endogeic species *Allolobophora rosea rosea* (Savigny, 1826) (0.7%) (Table 4). The litter (= food) was applied in at a rate of 434 g d.w. m<sup>-2</sup> year<sup>-1</sup> (= rate of disappearance). The four types of litter were (i) the natural herbs (H) produced by the spontaneous vegetation; (ii) a crushed wheat straw, the traditional agricultural residue in such a site (P); (iii) crushed lucerne (*Medicago sativa* L.) (L), as a rich litter, and (iv) natural litter from an evergreen oak (*Quercus ilex* L.) (C), the climax tree in this region. The litter-plots were prepared and studied from November 1985 to July 1987.

- The litter microcosms were kept under laboratory conditions to compare the earthworm ac-

## LAB technique experiment

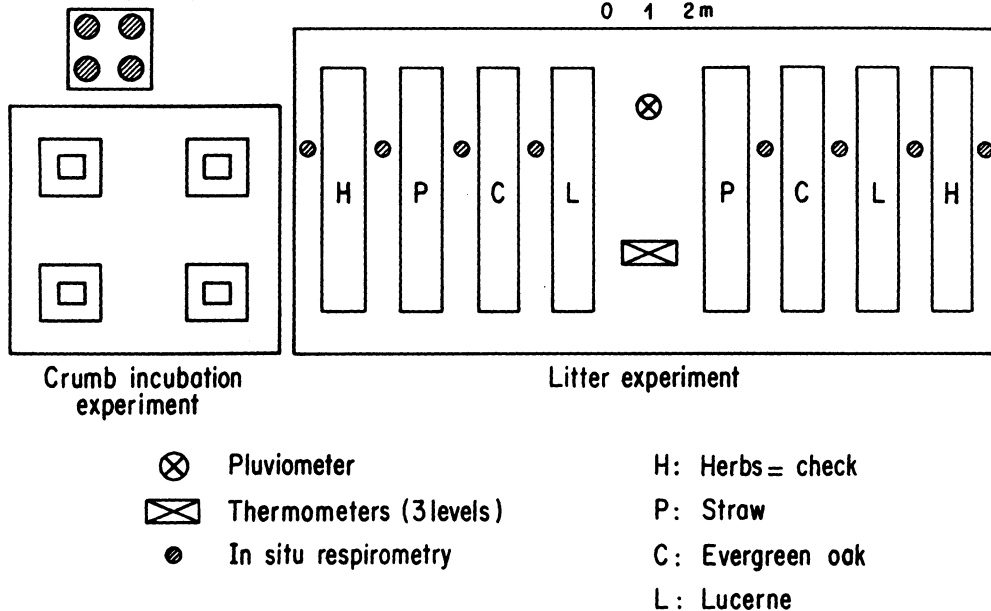


Fig. 4. General field arrangement of the various manipulated plots in the Larzat area.

Table 2. Individual and batch weight (g) of earthworms introduced in field microcosms (two replicates, with four individuals in each)

Weight in g	Herbs = H	Straw = P	Oak = C	Lucerne = L	Mean
Biomass in microcosms	42.1	39.3	45.2	41.2	42.0 (±2.4)

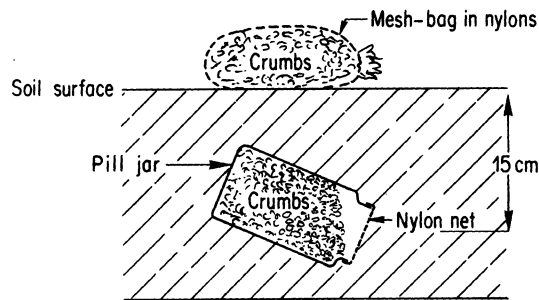


Fig. 5. Disposal of fresh faeces for incubation-stabilization in field, at top soil (as turricules) and in soil.

tivity with that in the field, especially with litter plots. In the field, earthworms use wide heterogeneity (see discussion); in the laboratory the aim was to reduce this heterogeneity to some extent. To do this eight buckets of 12 l were each filled with 9510 g of a dried soil from the field B horizon. This soil was sieved (5 mm) and then moistened to 9400 cm<sup>3</sup> (to achieve field density of 1.012). Moisture was brought to 80% of WHC (water holding capacity). The four litters (H, P, L, C) were used to feed four *Scherotheca mifuga* added to each bucket. These litter microcosms were studied from 3 December, 1985 to 13 July, 1987.

8. Crumb stabilization was studied with fresh faeces (surface casts) collected from the top of the soil from November 1985 to January 1986. Each faecal type (H, P, L, C) was air dried, homogenized,

divided into 13 × 3 fractions of 80 g d.w., moistened to 80% of WHC and used in three mesic conditions: (1) top soil field stabilization (as surface casts) by introduction in nylon mesh; (2) in soil field stabilization by introduction in a pill vial buried at a depth of -15 cm and air-opened into soil (Fig. 5); (3) in laboratory standard conditions (no light, 14°C, soil moisture kept at 80% of WHC).

The crumb incubation experiment started on 5 January, 1986 and was sampled on 13 dates during 536 days. After incubation the crumbs were analyzed for soil stability by the technique of Henin (1958). Air-dried soil was first gently crushed by a forced sieving through 2 mm holes, then aggregates between 2 and 0.2 mm were selected by sieving. These aggregates were first subjected to an alcohol treatment (= amphiphilic moistening) or a benzene treatment (lipophilic moistening).

These aggregates were then subjected to standardized disaggregation forces in water by the Feodoroff's apparatus (Feodoroff, 1960). The remaining aggregates were measured as a percentage of the initial soil (Aga %) for the alcohol treatment, which describes the fundamental cohesion (Cf) of moistened aggregates, and for the benzene treatment (Agb %), which describes the supracapillary cohesion (Cs) occurring in drying-hydration processes when capillary forces act against aggregate cement strength.

The carbon of the organic matter linked with minerals (Cl) was separated from the free or-

Table 3. Correlations and their significance (high = \*\*\*; very = \*\* or significant = \*) between the various characteristics observed on burrow nets

Correlation between	Pr	L <sub>gr</sub>	D <sub>s</sub>	D <sub>i</sub>	To	Sp	V <sub>o</sub>	N <sub>g</sub>	Pe	B <sub>i</sub>
Burrow depth (Pr)	-0.011									
Burrow length (L <sub>g</sub> )	ns									
Mean inter-distance (D <sub>s</sub> )	0.474	-0.834								
Mean diameter (D <sub>i</sub> )	0.491	0.027	0.203							
Net tortuosity (To)	-0.103	0.525	-0.559	-0.243						
Burrow surface (Sp)	0.157	0.942	-0.731	0.342	0.432					
Net volume (V <sub>o</sub> )	0.020	0.906	-0.776	0.368	0.381	0.971				
Number of burrow sticks (N <sub>g</sub> )	-0.171	0.968	-0.857	-0.017	0.544	0.886	0.887			
Percolation (Pe)	0.338	0.655	-0.450	0.417	0.129	0.770	0.679	0.542		
Earthworm biomass (B <sub>i</sub> )	-0.087	0.802	-0.744	0.229	0.384	0.837	0.859	0.835	0.604	
Number of individuals (N <sub>i</sub> )	-0.277	0.647	-0.833	-0.072	0.688	0.635	0.667	0.650	0.311	0.747

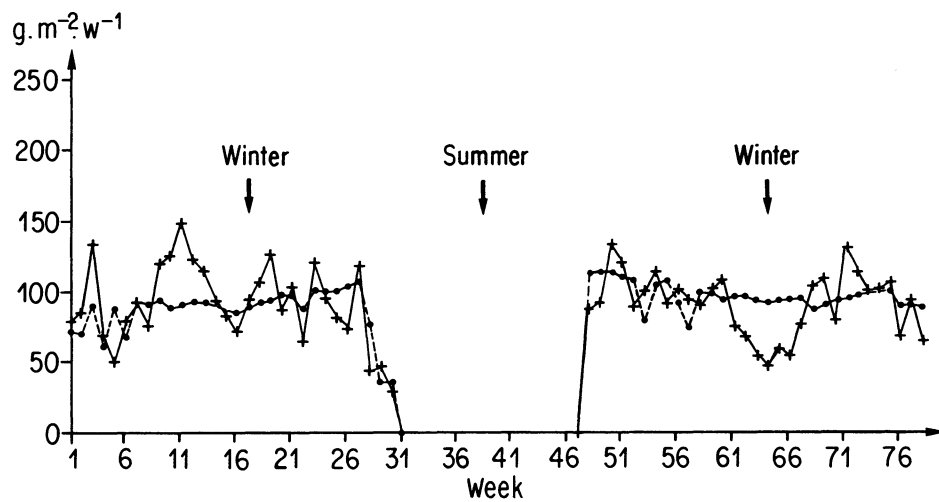
ganic matter by densimetry in BrZn (density 1.8) by a modified Tisdall (1980) method. The linked carbon fraction (Cl) was estimated with a Carmograph 12 Westoff apparatus (Bottner and Warembourg, 1976). Results are expressed as % of dry soil.

## RESULTS

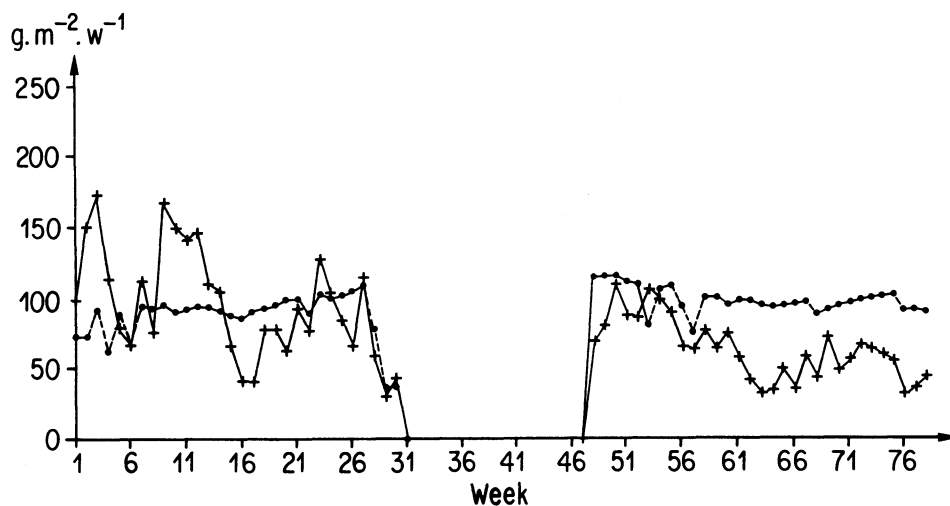
### Percolation rate and burrows

The infiltration rate and earthworm community biomass structure, measured in 17 sites of various mediterranean soils, led to a good correlation

between percolation and total earthworm biomass ( $n = 17$ ) and more closely with that of anecic species ( $n = 11$ ) (some communities lost their anecic species in cultivated soils: due to pesticides and machinery effects) (Al-Addan *et al.*, 1991). A closer study was made in the reference Larzat area on nine sites, where the active burrow systems were described. This study allowed us to compare percolation, earthworm biomass and earthworm burrow properties (Table 3). The burrow length was correlated negatively with the distance between burrows and correlated positively with burrow variables: stick number, parietal surface, net volume, earthworm biomass. Interdistance estimates confirmed



herbs = check +      S.M.A. simulation •



mean value of C.L.P. +      S.M.A. simulation •

Fig. 6. Weekly surface casting production observed in litter plots with the spontaneous herbs (top graph) and the mean values of the monospecific litters (oak, lucerne, straw). Comparison with the Sub-Model of Activity prediction.

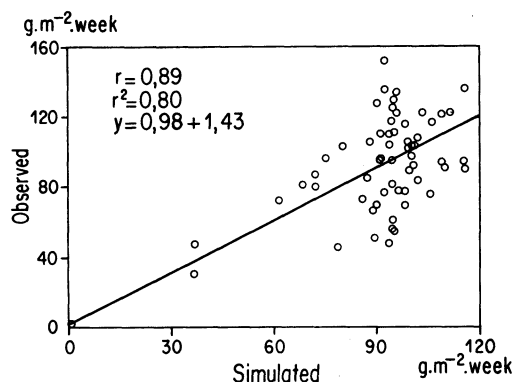


Fig. 7. Correlation between field observed and Sub-Model of Activity predicted turricule production in the spontaneous herb plot.

this figure, but clearly depended on the number of burrowing individuals. The tortuosity had no significant correlation with percolation, but depended on the number of individuals sharing the soil volume.

#### Effect of litter on earthworm population numbers and casting activity

Figure 6 presents the surface cast production in the four litter treatments over 78 weeks, a simulation made with SMA-REAL (Sub-Model of Activity of REAL) (Heidet and Bouché, 1991). The correlation between predicted and observed values with the natural litter (H-litter) was significant ( $r = 0.89$ ) (Fig. 7) All monospecific foods induced a decrease of surface cast production; a decline was observed at the end of the experiment (after an initial stimulation for lucerne and straw). In fact this reflects a decrease in the biomass (Table 4) which was observed at the end of the experiment and a rather regular decline of earthworm surface cast

production in comparison with the natural food (H) conditions.

#### Surface casting and in-soil faeces production by the LAB method

Table 5 presents surface casts and in-soil faeces produced in the field-microcosms under four treatments. Roughly 10 kg of faeces were produced by 1 kg of live earthworms  $\text{wk}^{-1}$ , with only 8.5% as surface casts.

The validation of the observable part of the system, i.e. surface casts in field-microcosms vs field conditions, shows a very good synchronism vs time (26 January 1987 to 30 April 1987) but an underestimation of the field-microcosm of 14% (herbs), 43% (wheat straw), 18% (Oak: *Q. ilex*) and 25% (lucerne). This could be explained by the decrease of earthworm feeding on foreign litters (straw, oak, lucerne) because the compared field plots were under treatment since November 1985, whereas the field-microcosms started on 26 January 1987 for 13 weeks. However this was not true for the H treatment (see 3.2). Two opposite hypotheses could explain this: (1) the earthworms are producing more faeces (both surface casts and in-soil) in field microcosms (= model bias), but the ratio of surface cast-to-in-soil is correct; (2) the initial soil destructuration (= absence of burrow) obliged earthworms to produce more surface casts in compacted soils (Bouché, 1975; Kretzschmar, 1989). In this interpretation, the total defecation is correct but only surface casts are over-estimated and conversely in-soil faeces deposition underestimated. These arguments (and others, see Al-Addan, 1992) led us to adopt an estimate based on field observations minus 10% and to accept a lack of precision of about 10%.

Table 4. Biomass ( $\text{g}\cdot\text{m}^{-2}$ ) observed in the four litter feeding treatments at the end of the experiment

	Mean biomass	Standard deviation	Significance
Herbs H	125.6	76.8	—
Straw P	83.3	63.0	—
Oak C	50.0	39.9	*
Lucerne L	109.3	66.1	—
Mean	92.0	65.4	

\*Significant.

Table 5. Field-microcosm measured faecal production and compared with surface casts produced in undisturbed soil ( $\text{g}\cdot 100\text{g}^{-1}$  viable earthworms  $\text{wk}^{-1}$ . Mean on 13 weeks)

	Herbs	Straw	Oak	Lucerne	Mean	
Field microcosms	Surf. casts	88.0	86.8	72.8	92.6	85.0
	In soil casts	948.7	885.9	973.4	859.3	916.8
	Sum	1036.7	972.7	1046.2	951.9	1001.9
	Ratio in soil/Turr.	10.8	10.2	13.4	9.3	10.9
	s.c. % um	8.5	8.9	7.0	9.7	8.5
Undisturbed turricules	75.3	60.5	59.3	68.8	66.0	
Surface casts difference % with control	-14.4	-30.3	-18.5	-25.7	-22.2	

Table 6. Change of Cs (Ag.b) and Cf (Ag.a) stabilities of crumbs before and after 536 days of incubation. Comparison in % with the A<sub>1</sub> horizon

		Stability before incubation		Field surface		Stability after incubation		Lab. microcosm	
		Ag.b%	Ag.a%	Ag.b%	Ag.a%	Field - 15 cm Ag.b%	Ag.a%	Ag.b%	Ag.a%
% Stable aggregates	Herbs	21.5	63.9	56.2	64.7	74.6	78.9	61.9	71.5
	Straw	15.3	61.6	41.8	61.3	63.4	69.2	37.1	61.9
	Oak	18.7	63.1	55.4	62.4	65.2	77.1	76.3	78.8
	Lucerne	33.1	66.2	61.7	67.2	79.1	81.1	53.8	70.8
	Mean	22.2	63.7	53.8	63.9	70.6	76.6	57.3	70.7
% of the A <sub>1</sub> horizon properties	Herbs	-59.7	6.5	5.2	7.9	39.7	31.6	15.9	19.2
	Straw	-71.3	2.8	-21.8	2.2	18.7	15.3	-30.5	3.2
	Oak	-64.9	5.3	3.7	4.0	22.1	28.5	42.8	31.4
	Lucerne	-38.1	10.4	15.6	12.0	48.0	35.2	0.7	18.0
	Mean	-58.5	6.2	0.7	6.5	32.2	27.7	7.2	18.0

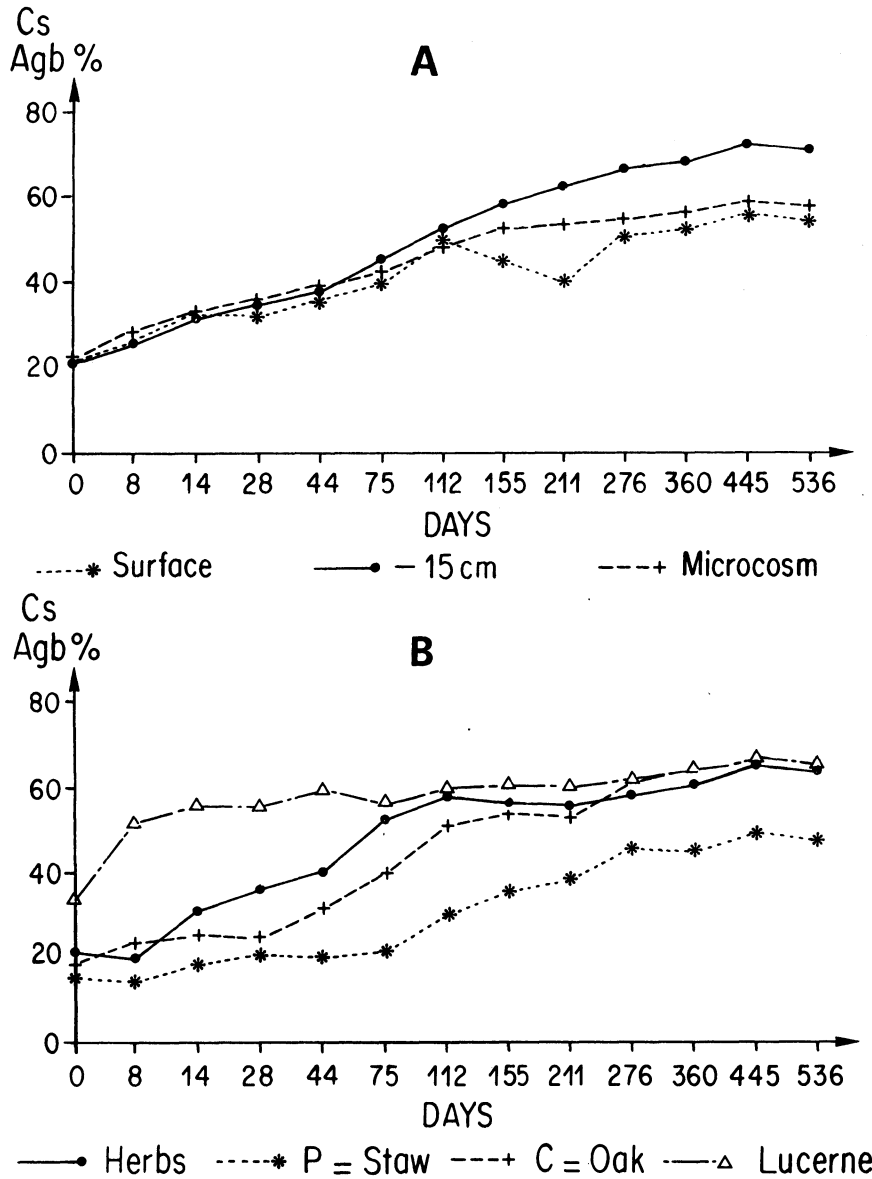


Fig. 8. Evolution of the supracapillary cohesion of earthworm crumbs during 536 days. A = mean values of the four foods; B = mean values of the three mesic conditions (top soil, 15 cm depth, in laboratory).

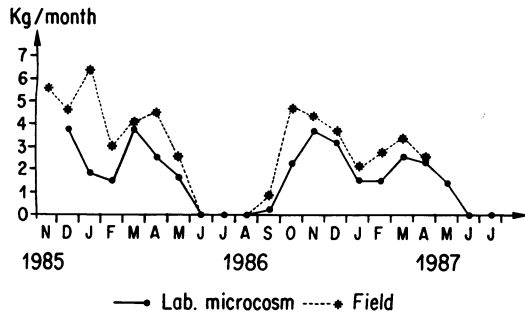


Fig. 9. Seasonal turricule production ( $\text{kg}^{-1}$  kg earthworms month) observed in the field (Nov '85 to April '87) and in the laboratory (Dec. '85 to July '87). Notice the memory of field variations in constant laboratory conditions.

and the four litters used. R% gives the relative change in % of the  $A_1$  horizon values. We use  $A_1$  because most of the mineral soil ingested by anecic species came from this horizon (Bouché *et al.*, 1983). This expression is partly inaccurate and rather conventional. Figure 8 shows the evolution of Cs stability in each treatment condition and in each food. The change between initial and final organic matter (total, free, linked) is given in Table 7 (also compared with the A horizon). The change of the C-to-N ratio is presented in Table 8.

#### Seasonal change in crumb production

Seasonal moisture and temperature change in soil were parallel and Fig. 6 shows the seasonal surface cast production changes observed and simulated (SMA-REAL) (food: natural herbs). Parameter of the SMA-REAL submodel was calibrated with soil temperature and moisture gradients, and the photoperiod vs motility induced by formalin applications in field (Heidet and Bouché, 1991). In the laboratory, in stable moisture and temperature conditions and with no light, *S. mifuga* kept up a seasonal rhythm (Fig. 9) simulating field observations.

## DISCUSSION

The work presented in the previous section is based mostly on a study (Al-Addan, 1992) presented as a thesis in July 1991. Fathel Al-Addan went back to Iraq for his military service just at the start of the Arabian Gulf confrontation. Since we

have no news about him; this discussion is made only under the responsibility of the senior author.

#### Homeostasy versus heterogeneity

Earthworms are heterochrestic. [Heterochresty from the Greek, heteros = different, and chrestikos = knowing how to use (Brown, 1956)]. The heterochresty is the aptitude to use the heterogeneity.

Earthworms use the heterogeneity vs the three ecological referencers i.e. space, time and composition. *In space*, earthworms dig subvertical burrows to use the vertical thermic and moisture heterogeneity in order to live as close as possible to their optima (Bouché, 1987; Heidet and Bouché, 1991), to organize chambers for cocoons (Lamparsky, 1985) and to store their casts as future food (Bouché *et al.*, 1983, 1987). *In time*, true anecic species regulate their diapause through an endocrinal photoperiodic control (Saussey and Debout, 1984; Bouché, 1984) if the animal registers its biorhythm for a few months, but not on some days as observed by Galissian (1971). *S. mifuga* having a very long life span and registering their habitat conditions for at least 1–2 years, kept their rhythm until the laboratory experiment ended after 18 months. Astonishingly, this rhythm not only reflects the diapause, but also the cold season at a controlled temperature (Fig. 9). *In composition* earthworms use the heterogeneity of their milieu. They select their food carefully (Darwin, 1881). Including the field where a great heterogeneity was preserved they finally lost weight and casting efficiency in all of the homogenized food treatments and kept normal in the two life indicators using the heterogeneous food: the natural herb mixture. Conversely, in a homogenized soil, Randriamamonjizaka (1984), illustrated a food choice in making comparison of a soil before ingestion and after casting: the organic fraction increased apparently during the gut transit including the coarse fraction, despite the gizzard comminution and digestion (Table 9). The heterochresty interfered in the laboratory as observed with the conservation of the biorhythm and led to interference in lab-microcosm studies, as observed by Galissian (1971), who saw a spontaneous diapause of *S. gigas galissiani* (Bouché and Beugnot, 1972) 51 days after the isolation of this species under constant laboratory conditions.

Table 9. Selection of faeces made by *Lumbricus terrestris* L. in two homogenized soils (faeces produced in dark culture chamber) (unpublished Randriamamonjizaka, 1983)

	C and N % of dry soil			Fractions of % org. matter		
	C	N	C to N	> 100	100–50	< 50
<i>Silt soil</i>						
microcosm soil faeces	36.9	2.3	16.0	19.0	28.7	52.3
	45.6	2.9	15.7	19.9	22.8	57.3
<i>Terra fusca</i>						
microcosm soil faeces	32.2	2.4	13.4	15.3	20.5	64.2
	41.1	2.5	16.4	15.0	16.7	68.3



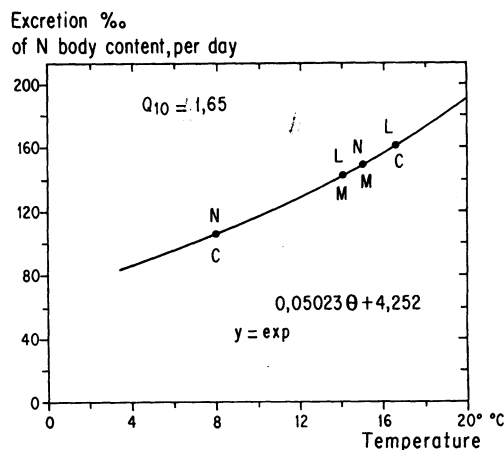


Fig. 10. Nitrogen excretion rate measured in field (C) or in microcosms (M) on *Nicodrilus longus* Ude (N) and *Lumbricus terrestris* (L) in various temperature conditions (moisture and photoperiod were not limiting factors) (see Bouché *et al.*, same symposium) (four estimations grounded on 81 isotope ratio measures).

#### Metabolism, physical behaviour and microcosm studies

In microcosms, when earthworms survive close to their steady state (no individual weight change), their metabolism was similar to that in the field. A comparison of the observations made by Ferrière (1986) and Hameed (1989) with  $^{15}\text{N}$  labelled earthworm belonging to two anecic genera, controlled in two laboratory conditions or living in two fields, demonstrated a sole function for anecic species nitrogen daily exchanges (excretion balanced by assimilation) depending only on temperature (Fig. 10).

Conversely, the earthworm soil physical work was not validated. To keep at least their steady state earthworms compensate for the homogeneity in microcosms by (1) the priority of their genetical life control (assimilation, excretion), including their seasonal endocrinal memory; (2) the use of the remaining heterogeneity by an abnormal soil working (= compensating behaviour). This soil working interferes with microbial activity, which could induced very different results such as the effect of organic mixing in soil. Here we observed a very good assimilation-excretion estimation by lab-microcosm simulation and a great underestimation of cast production (Fig. 9).

In conclusion, if earthworms were kept in a steady state in microcosms, they used, due to an abnormal soil work, the remaining heterogeneity (moisture, food and soil components) to preserve a normal metabolism (that is their priority) compensating spatiotemporal man-created artifacts such as soil crushing, mixing and factor homogenization. In good conditions (at earthworm steady state) microcosm models led to predictions being validated in the field for metabolism only, thanks to the het-

erocrestic earthworm behaviour into an homogenized microcosm milieu. Conversely this behaviour creates a non validated physical activity.

#### Soil water infiltration

The water percolation rate was  $150 \text{ mm h}^{-1} 100 \text{ g}^{-1}$  of fresh earthworm biomass, 10 or more closely to  $282 \text{ mm h}^{-1} 100 \text{ gm}^{-1}$  of anecic species. That is probably far greater than that needed for soil infiltration in the heaviest rain of most storms (at least in the erratic mediterranean perhumid climate). Nevertheless, we occasionally had catastrophic run-off, eroding soil and killing of inhabitants. This could be due to three situations:

1. *The lack of deep drainage.* Earthworms naturally connect their burrows on artificial or natural deep drain (as agricultural drainage or karstic fractures) (Urbanek and Dolezal, 1992; Heidet, *in litt.*). In our study in a geological karstic situation, this deep drainage was not a limiting factor and the percolation occurs with a good anecic correlation. This was not the case with a previous study of Assad (1987) made in some soils without deep drainage. Infiltration started well but percolation was sometimes restricted by the deep soil infiltration which did not depend on earthworms.
2. *The lack of earthworms.* Another study demonstrates in south-east France the lack of anecic species, and especially the eradication of the gigantic *Scherotheca*, induced by heavy metal soil contamination (Abdul Rida and Bouché, 1994). This occurs unfortunately in a rather wide surface area: the vinyard area was deeply polluted by copper sulphide spraying against pathogenic fungi.
3. *The post-drainage effect.* In a large storm, water can percolate through earthworm channels then, through connected artificial or natural drainage and after contributes to a general overflow by an artesian resurgence.

Except in situation 1b earthworms play a key rôle in water infiltration, avoiding or restricting. The catastrophic run-off and improved soil water reserves which is also improved by the interstitial space between crumbs and the water-holding capacity of earthworm crumbs.

#### Crumb origin and turn-over

Darwin (1837) correctly pointed out the importance of earthworms in creating a granular soil (mould). Despite this, most soil scientists attribute crumbs to root action, especially because a root network extracted from a mull offers often crumbs attached to fine roots. This was criticized by careful studies by Stewart and Scullion (1988). Here we extracted all crumbs by soil sieving (sieve mesh = 2 mm) and we observed them by macro-

morphology. There was always a close mixing of figured organic matter and minerals. In fact, knowing the crumb production in the field ( $36.6 \text{ kg m}^{-1} \text{ y}^{-1}$ ) and the observed crumbs in the herb treatments ( $83.7 \text{ kg m}^{-2}$ ), we can assume that, if earthworms do not re-ingest their faeces, the crumble turn-over is  $83.7/36.6 = 2.29$  year. We know that anecic species re-ingest about 50% of their casts (Bouché *et al.*, 1983) and this after a delay of some months (Bouché *et al.*, 1987) as observed by  $^{14}\text{C}$  litter labelling in the field by Dietz (1977). We can conclude that the mean faeces turn-over is about 26–28 months while the crumb age is about double this (about 4 years). Crumb origin could be observed by micromorphology (Al-Addan, 1992) and better observed by labelling (that was not done here).

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