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Effects of a tropical geophagous earthworm, *Millsonia anomala*, on some soil characteristics, on maize-residue decomposition and on maize production in Ivory Coast

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Abstract

Maize was grown under field conditions in the presence and absence of the tropical endogeic earthworm *Millsonia anomala* (Omodeo and Vaillaud, 1967) in soil of a secondary forest of central Ivory Coast. Experimental units were isolated by PVC sheets to limit earthworm movements. Decomposition and redistribution of nitrogen from maize crop residues incorporated in the soil were monitored using ^{15}N-labelled residues.

The density of *M. anomala* decreased from 50 to 15.9 m^{-2} during the cultivation period (90 days). Activity of *M. anomala* significantly modified the structure of the soil by increasing the proportion of large aggregates (over 2 mm in diameter). Maize production was increased by 12% for stalks and 18% for grains in the presence of earthworms. Nitrogen contained in the maize residue was more efficiently used by plants grown in the presence of earthworms; the real coefficient of utilisation of the organic residue increased from 9 to 11% in the presence of *M. anomala*. Nonetheless, total nitrogen exportation was not significantly different between the two treatments. Furthermore, N from the organic residues left after the cultivation period was less easily assimilated by plants in treatments with earthworms.

Keywords: Earthworms; Tropics; Maize; ^{15}N; Soil physical characteristics

1. Introduction

Tropical geophagous earthworms significantly affect the physical structure of soil (Aina, 1984; Lee and Ladd, 1984; Lal, 1988; Blanchart et al., 1990); they also have major effects on soil organic matter dynamics (Martin, 1991a; Lavelle and Martin, 1992). Earthworms through their feeding and mechanical activities have a strong impact on decomposition of plant residues. At the scale of fresh casts following deposition for a few weeks, they generally accelerate mineralisation. Furthermore, soil aggregation, the structure of porosity and connectance among pores are significantly changed (Blanchart, 1990). All these factors may affect plant production. Several studies, in culture pots, have demonstrated some improvement in cereal and grass yields due to the addition of temperate-climate earthworms (Van Rhee, 1965; Atlavinyte, 1974). However, very little is known of the effects of non-lumbricid earthworms on plant pro-

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duction. In a preliminary pot experiment conducted in Ivory Coast, inoculation of soil with earthworms resulted in a significant increase in maize and grass production (Spain et al., 1992). An experiment was set to test the hypothesis that enhanced decomposition of ^{15}N labelled maize residues mixed with the upper few centimetres of soil and changes in soil physical structure resulting from earthworm activities positively affect maize production. This experiment was part of a research project aimed at assessing the effects of geophagous earthworms, *M. anomala* and *Pontoscolex corethrurus*, on the production of tropical annual plants (Lavelle et al., 1992).

2. Materials and methods

2.1. Study site and experimental design

The study was carried out at the Ecological Station of Lamto, Ivory Coast (5°N, 6°W, elevation 105 m). Climate is characterised by a high average annual temperature (28.8°C) and irregular annual rainfall (30 year average 1200 mm year^{-1}), with dry seasons from November to March and in August (Pagney, 1988).

Soils are tropical ferruginous (ferralsols, FAO–UNESCO classification) derived from granitic parent material. In the experimental plot, soil was sampled for chemical analyses in December 1991, prior to maize cultivation. Soil texture is sandy and the clay content is low (Table 1). Organic and nutrient contents are low and they decrease very rapidly from the upper soil layer to 40 cm depth.

Natural vegetation is a mosaic of grass savannas and woodlands (César and Menaut, 1974). The experiment was carried out in a secondary forest belonging to the *Celtus–Triplochiton* formation (Gilot, 1994). The soil macrofauna is largely dominated by earthworms (Athias et al., 1974), especially geophagous species that comprise a biomass of 26–43 g m^{-2} fresh weight depending on shrub density (Lavelle, 1978). The dominant species is *Millsonia anomala*, a mesohumic endogeic that lives mainly in the upper 20 cm of the soil (Lavelle, 1981). Adults may reach 17 cm in length and weigh up to 4 g fresh weight. *M. anomala* is less abundant in the forest than the savanna (32 m^{-2} and 19 m^{-2}, respectively, in December 1992).

The experimental plot (19 m × 16 m) was installed in a secondary forest. Twenty four microplots, 0.8 m × 1.6 m in size, were isolated by inserting thick PVC sheets in the soil to a depth of

Table 1
Texture and chemical characteristics of the experimental soil to 40 cm depth (means ± SE)

	Soil depth (cm)			
	0–10	10–20	20–30	30–40
Sand (%) [a]	85.0 ± 4.0	86.3 ± 2.0	86.7	ND
Loam (%)	10.5 ± 3.0	11.3 ± 1.2	10.3	ND
Clay (%)	4.5 ± 1.4	2.4 ± 1.2	4.2	ND
C (%) [b]	1.18 ± 0.07	0.48 ± 0.05	0.28	0.21
N (‰)	1.20 ± 0.07	0.57 ± 0.05	0.40	0.29
pH (water) [c]	7.15	6.65	6.20	5.65
P Olsen (ppm)	8.32	7.59	6.79	5.00
Ca (cmol kg^{-1})	4.53	2.04	1.05	0.60
Mg (cmol kg^{-1})	0.88	0.51	0.39	0.32
K (cmol kg^{-1})	0.23	0.07	0.06	0.04
EECC (cmol kg^{-1})	5.34	2.80	1.67	1.12

[a] Five replicates for determination of texture to 20 cm depth and one replicate (composite sample) for the stratum 20–30 cm.
[b] Five replicates for C and N contents to 20 cm depth and one replicate (composite sample) for the strata 20–30 and 30–40 cm.
[c] Composite samples were used for the determination of other parameters (no replicates).

50 cm, leaving a rim of 10 cm above the surface level. Each microplot was divided (with a PVC sheet) into two parts that comprised one-third and two-thirds of the total surface area, respectively. Destructive samplings were done during the growing period in the smaller part. On each of the two sampling occasions, three different pairs of enclosures were sampled. At harvest, the larger parts of all microplots were sampled.

Soil of the enclosures had been previously sieved at 2.5 mm by successive strata of 10 cm down to 40 cm depth and air dried to eliminate the worms. A plastic mosquito net was placed at the bottom of the enclosures to avoid colonisation by native worms from deeper strata.

Maize residues were incorporated into the upper 10 cm of the soil 7 days before sowing. Each experimental unit received the equivalent of 1.6 t ha^{-1} of fragments 1–2 cm long. In three pairs of microplots, the residue added had been previously labelled with ^{15}N (Table 2). The residue is supposed to be homogeneously labelled. The labelled and non-labelled residues were produced in pots at Lamto experimental station.

Populations of the endogeic earthworm *M. anomala* were introduced at a high density (50 m^{-2}) and biomass (40 g fresh weight m^{-2}) in half of the units (named MA +). Special attention was paid to the relative proportions of adults and juveniles (Table 3). Introduction was carried out 5 days before sowing.

Maize was sown at a high density of 18 plants per enclosure (equivalent to 140000 plants ha^{-1}) to maximise plant demand for nutrients. Composite seeds were used (Ferké 8128). Plants were grown without chemical fertilisers or pesticides. Microplots were kept clean by manual weeding every 15 days.

Parameters measured during the cycle or at harvest comprised above-ground production of maize, density and biomass of earthworms, recovery of ^{15}N in the different compartments (soil, plant) and soil physical and chemical analyses.

Table 2
Characteristics of labelled litter

	N content (%)	Isotopic excess ^{15}N (%)	Added material (g m^{-2})
Stalks	2.65	4.87	116.0
Leaves	3.08	4.77	42.6
Total	2.77	4.84	158.6

2.2. Field and laboratory analyses

2.2.1. Earthworm sampling (35, 70 and 90 days after sowing)

Earthworms were collected by hand-sorting the soil to 40 cm depth. Specimens of *Millsonia anomala* and other species were counted and weighed alive.

2.2.2. Maize production (35, 70 and 90 days after sowing)

Plant components (stalks, ears, grains) were collected separately, oven-dried (105°C) and weighed.

2.2.3. Soil sampling (70 days after sowing)

The totality of the soil of each experimental unit was thoroughly mixed and homogenised separately in the upper two strata (0–10 and 10–20 cm depth) after hand-sorting the earthworms and 3-kg samples were taken in each stratum. Then, soil was air dried and sieved through a 2 mm mesh; a 200 g aliquot was homogenised and kept for analyses.

2.2.4. Soil and plant nitrogen (70 days after sowing)

Three different fractions of total soil nitrogen were separated by acid hydrolysis (Stewart et al., 1963; Egoumenides, 1989; Waneuken and Ganry, 1992):

1. non-hydrolysable nitrogen (Nnh);
2. hydrolysable distillable nitrogen (Nhd);
3. hydrolysable non-distillable nitrogen (Nhnd).

Soil was hydrolysed with 6 N HCl for 6 h. The hydrolysate was further distillated in an alkaline medium (NaOH added) and N content of the hydrolysate determined by acidometric titration (Nhd). Total N in the hydrolysate was determined by the Kjeldahl procedure. The difference between total N and the distillable acid-soluble nitrogen fraction (Nhd) was designated hydrolysable non-distillable N (Nhnd). The third organic N fraction (Nnh) was obtained by Kjeldahl mineralisation of the acid insoluble residue. Isotopic excess of every N fraction was measured.

The hydrolysable non-distillable nitrogen (Nhnd) is mainly composed of amino acids produced by

Table 3
Mean density (m^{-2}) and biomass (g fresh weight m^{-2}) of *M. anomala* and other earthworms in experimental units (with (MA +) and without (MA −) *M. anomala*) at the different sampling dates

				Day 0	Day 35	Day 70	Day 90
MA +	*M. anomala*	Density	Juveniles	30	24	5	8.5
			Adults	20	21	2	7.4
			Total	50	45	7	15.9
		Biomass	Juveniles	11.8	15.2	0.2	0.55
			Adults	28.2	26.9	2.1	7.90
			Total	40.0	42.1	2.3	8.45
		Mean weight	Juveniles	0.39	0.63	0.04	0.07
			Adults	1.34	1.28	1.06	1.06
	Others	Density		0.0	2.4	13.4	15.6
		Biomass		0.0	1.60	3.07	3.98
MA −	*M. anomala*	Density		0.0	2.0	2.0	0.4
		Biomass		0.0	2.45	3.25	0.40
	Others	Density		0.0	0.0	34.6	11.4
		Biomass		0.0	0.0	4.61	2.95

microbial catabolism. Nitrogen from the hydrolysable distillable fraction originates from hexosamines and amides of certain amino acids. The Nnh fraction that is less well characterised would mainly comprise heterocyclic nitrogen (Stewart et al., 1963; Jocteur Monrozier and Andreux, 1981).

Nitrogen derived from labelled litter (Ndfll) and the real utilisation coefficient (RUC) of this residue were calculated to determine whether earthworm activities improve the utilisation by the plant of N from decomposing litter. Values are calculated using the following equations (Ganry, 1990):

1. percentage of the total plant nitrogen derived from labelled litter

$$\text{Ndfll}(\%) = \frac{E_{pl}}{E} \times 100$$

2. percentage of nitrogen of the labelled litter uptake by the plant

$$\text{RUC}(\%) = \frac{Q_n \times E_{pl}}{F \times E} \times 100 = \frac{Q_n}{F} \times \text{Ndfll}$$

where Q_n is total nitrogen in the plant (g m^{-2}), E_{pl} is isotopic excess of the plant (%), F is total nitrogen in labelled litter (g m^{-2}) and E is isotopic excess of labelled litter (%). N contents and isotopic excesses were measured in four plant components (stalks, leaves, ears and roots).

2.2.5. Aggregation (90 days after sowing)

The size distribution of soil aggregates at harvest was assessed by dry sieving monoliths (20 cm × 20 cm × 20 cm) in five replicates per treatment. After monoliths had been separated into two layers (0–10 and 10–20 cm) they were separately broken into large blocks (about 800 cm^3) and air-dried to a moisture content of about 5–6% dry weight (pF ≈ 4). Aggregates were separated by dropping the air dried blocks from a constant height of 1.5 m onto a hard surface (Blanchart, 1992). Fragments were further air dried and sieved on meshes of the following sizes: 10 mm, 6.3 mm, 5 mm, 2 mm, 1 mm, 630 μm, 500 μm, 400 μm, 315 μm, 250 μm. Separated fractions were weighed.

2.2.6. Water infiltration (90 days after sowing)

Water infiltration rate was measured in the same units as soil aggregation. Leaf litter was removed from the soil surface. A plastic ring (25 cm in diameter and 40 cm high) was driven vertically 15 cm into the wet soil. The cylinder was filled with water to 20 cm above soil level. Distance of the

water level to the cylinder top was recorded during 1 h (adapted from Anderson and Ingram, 1992).

2.2.7. Maize residue decomposition

Decomposition of the maize residue was measured during a period of 8 weeks. The soil was removed from cylinders (20 cm diameter, 20 cm depth). Wire netting (0.1 mm mesh) was driven vertically to the bottom of the hole and a mosquito net placed at the bottom to avoid invasion by native worms. Maize residues (110 g m^{-2}; fragments 1–2 cm long) were mixed into the upper 10 cm soil layer in the small enclosures. In half of the enclosures, two young *M. anomala* were introduced. Three replicates per treatment were sampled every week. Soil organic matter over 2 mm in size was separated by flotation and maize residues were sorted under a stereo microscope, oven-dried (105°C) and weighed. Maize residues less than 2 mm in size were not recovered.

3. Results

3.1. Earthworms

The density of *Millsonia anomala* populations at harvest decreased significantly from 50 to 15.9 m^{-2} over the course of the experiment (Table 3). Density of *M. anomala* in the non-inoculated treatment remained less than 2 m^{-2}. Since the number of earthworms of other species found in the units increased

Table 4
Effect of earthworm inoculation on the distribution of aggregates (mean values) of different size classes (with (MA +) and without (MA −) *M. anomala*) in the 0–10 and 10–20 cm strata at the end of the experiment

Aggregate size class	Depth (cm)	MA − ($n = 9$)	MA + ($n = 9$)	P (Student's test)
0–250 μm	0–10	21.7	16.7	< 0.05
	10–20	17.0	16.6	NS
250–315 μm	0–10	4.3	3.3	< 0.05
	10–20	3.8	3.6	NS
315–400 μm	0–10	13.2	9.4	< 0.01
	10–20	12.0	10.9	NS
400–500 μm	0–10	9.0	7.0	< 0.05
	10–20	8.5	8.3	NS
500–630 μm	0–10	7.6	5.4	< 0.05
	10–20	7.6	6.8	NS
630 μm–1.0 mm	0–10	12.4	9.7	< 0.01
	10–20	12.8	11.3	NS
1.0–2.0 mm	0–10	7.0	6.3	NS
	10–20	7.6	6.3	NS
2.0–5.0 mm	0–10	5.6	6.6	NS
	10–20	5.7	4.8	NS
5.0–6.3 mm	0–10	1.6	2.6	NS
	10–20	1.7	1.8	NS
6.3–10 mm	0–10	6.2	13.2	< 0.01
	10–20	6.8	8.6	NS
> 10 mm	0–10	11.2	19.9	< 0.01
	10–20	16.5	20.9	NS
Σ(0–0.4 mm)	0–10	39.3	29.4	< 0.05
	10–20	32.8	31.2	NS
Σ(0.4–2 mm)	0–10	36.1	28.3	< 0.01
	10–20	36.5	32.7	NS
> 2 mm	0–10	24.6	42.2	< 0.01
	10–20	30.7	36.1	NS

NS, not significant.

Table 5
Maize production: vegetative parts and grains, number of grains, weight of 250 grains and proportion of fertile plants at the different sampling dates (with (MA +) and without (MA −) *M. anomala*) (probability values are given for unilateral *t*-test on paired values)

	Day 35			Day 70			Day 90		
	MA −	MA +		MA −	MA +		MA −	MA +	
Stalk production (g per plant)	5.0	5.1	NS	44.0	41.4	NS	57.0	64.0	< 0.05
Grain production (g per plant)							18.1	21.4	< 0.10
Weight of 250 grains (g)							31.1	33.8	< 0.05
No. of grains (per ear)							184	198	NS
Proportion of fertile plants (%)							64	65	NS

NS, non-significant difference between MA + and MA − .

with time from 0 to 15.6 m^{-2}, it is believed that they progressively colonised the units from the outside (Table 3).

Changes in the demographic structure of the population of *M. anomala* give some clues to the interpretation of changes observed in the earthworm populations. During the first 35 days no great changes occurred (Table 3). However, after 65 days, the density of juveniles and adults was substantially reduced. Most juveniles found at this time were only 1–4 weeks old, suggesting that the reproduction period had occurred some 40 days after introduction of the earthworms and, later on, density had decreased sharply since a large number of worms had died or possibly escaped.

3.2. Soil structure

At harvest, aggregate size distribution was significantly different in the two treatments only in the 0–10 cm depth strata (Table 4), indicating that earthworms had concentrated their activity in the upper soil layer. The proportion of aggregates larger than 2 mm was increased from 24.6% in the non-inoculated treatments to 42.2% in the inoculated treatment. Furthermore, earthworm activities significantly increased the proportion of larger aggregates (over 6.3 mm diameter). These classes of aggregates were mainly composed of casts of *M. anomala* in treatments with earthworms. On the other hand, all classes of aggregates smaller than 1 mm were represented significantly less in the presence of earthworms.

3.3. Water infiltration

Water infiltration in soil was significantly reduced (by 25%) in the presence of *M. anomala*. In 1 h, the quantity of water infiltrated was 200 mm and 250 mm in the MA + and MA − enclosures, respectively.

Table 6
Elements of the N budget of maize plants: N contents in plant, N derived from labelled litter (Ndfll) and percentage of nitrogen of the labelled litter taken up by the plant in the different parts of the plant (RUC) (with (MA +) and without (MA −) *M. anomala*)

	N content (%)		Ndfll (%)		RUC (%)	
	MA −	MA +	MA −	MA +	MA −	MA +
Stems	0.43	0.48	5.50	6.44	1.45	1.73
Leaves	1.56	1.70	4.90	5.68	6.40	7.85 *
Ears	1.22	1.14	4.83	5.89	0.71	0.99
Aerial parts	1.07	1.19	4.99	5.86	8.56	10.58 *
Roots	0.61	0.60	7.36	6.24	0.46	0.37 *
Whole plant	1.05	1.15	5.09	5.88	9.03	10.95 *

Student's *t*-test: * $P < 0.10$.

3.4. Maize production

Maize was planted at a density equivalent to 140000 plants ha^{-1}. Mean yields were 2.8 t ha^{-1} for grains and 8.4 t ha^{-1} for stalks (Table 5). The ratio of grains to stalks was very low (0.33). The high plant density induced huge competition between plants and only 65% of plants produced ears.

Significant differences for stalk yields at harvest were observed between treatments; stalk production was increased by 12% in the presence of earthworms. The increase in grain yield was 18% ($P < 0.1$) in the inoculated units and the weight of 250 grains was significantly higher. The number of grains and the proportion of fertile plants were not significantly different between the two treatments.

No significant difference of production was observed between the two treatments at intermediate sampling dates.

3.5. Decomposition of the maize residue

Disappearance of maize residues larger than 2 mm was rapid, in the presence and absence of *M. anomala* (Fig. 1). After 14 days, only 20% of the initial material had been recovered. It is likely that a large proportion of residues had only been fragmented at that stage and still little decomposed. The presence of earthworms had no significant effect on the rate of decomposition.

3.6. ^{15}N incorporation in plants

The N content of plant material was not different in the two treatments 70 days after sowing (Table 6).

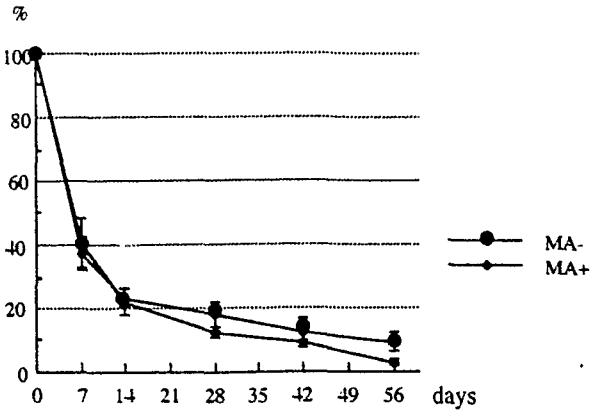

Fig. 1. Percentage of maize residue over 2 mm in diameter remaining in the presence (MA+) and absence (MA−) of *M. anomala*.

The percentage of plant nitrogen derived from the labelled material was not significantly different in the two treatments for stems, leaves, ears and roots, even if it was higher in the presence of earthworms (except for the roots). However, the quantity of nitrogen derived from the labelled material was slightly higher (not significant at $P < 0.05$) in stalks and ears in inoculated treatments. Plants grown in the presence of *M. anomala* had accumulated more nitrogen derived from the labelled litter in their aerial parts. Furthermore, the real coefficient of utilisation (RUC) of the organic residue was significantly increased by more than 20% in the presence of earthworms.

3.7. ^{15}N in soil

The overall content and distribution of N among the different fractions were assessed in December 1991 and July 1992, respectively 5 months before,

Table 7
Distribution of soil N between the N fractions before and after the cropping cycle (December 1990 and July 1991) expressed in ppm (with (MA +) and without (MA −) *M. anomala*)

	0–10 cm						10–20 cm					
	December 1990			July 1991			December 1990			July 1991		
	MA −	MA +		MA −	MA +		MA −	MA +		MA −	MA +	
Nnh	248	283	NS	226	235	NS	133	161	NS	125	136	NS
Nhnd	570	624	NS	547	556	NS	273	323	NS	256	274	NS
Nhd	160	169	NS	162	163	NS	68	76	NS	70	73	NS
Total	978	1076	NS	935	954	NS	474	560	NS	451	483	NS

Nnh, non-hydrolysable nitrogen; Nhnd, hydrolysable distillable nitrogen; Nhd, hydrolysable non-distillable nitrogen.
NS, non-significant difference between MA + and MA − .

Table 8
Percentage of ^{15}N recovered in the soil in each N fraction at two depths (Student's *t*-test, * $P < 0.05$) (with (MA+) and without (MA−) *M. anomala*)

	0–10 cm			10–20 cm		
	MA−	MA+		MA−	MA+	
Nnh	7.2	7.7	NS	0.8	1.4	*
Nhnd	39.9	27.7	*	2.9	6.0	NS
Nhd	3.8	4.4	NS	0.3	0.6	*
Total	51.0	39.8	*	4.0	8.0	*

Nnh, non-hydrolysable nitrogen; Nhnd, hydrolysable distillable nitrogen; Nhd, hydrolysable non-distillable nitrogen.
NS, non-significant difference between MA+ and MA−.

and 70 days after sowing. Some differences were observed between inoculated and non-inoculated plots, but none were significant (Table 7). Soil nitrogen content decreased from 1.03 to 0.94‰ in the 0–10 cm depth stratum during this 7 month period (means between the two treatments). The most labile nitrogen, present in the Nhd and Nhnd fractions had decreased in the two strata. Nitrogen present in the Nnh fraction remained constant.

The amount of ^{15}N recovered in soil (strata 0–10 + 10–20 cm) was not significantly different between treatments and was about 50% of the N added with the labelled material. However, ^{15}N was located significantly deeper in the soil of inoculated treatments (Table 8).

The distributions of N derived from the labelled material recovered in soil among fractions were compared in the presence and absence of earthworms (Table 9). In both treatments, N derived from the labelled residue was mainly recovered in the Nhnd. The proportion of this fraction was higher in the N derived from the maize residue than from the whole soil.

Furthermore, there was an effect of the activity of earthworms on the distribution of the N from the maize residue in the chemical N fractions: in the 0–10 cm stratum, the relative proportions of Nhd and Nnh were increased in inoculated treatments, whereas the Nhnd fraction was decreased. No significant differences were observed between treatments in the 10–20 stratum.

4. Discussion

The effects of *M. anomala* on soil structure were in accord with the results of Blanchart (1990) and Blanchart (1992). The reaggregation of soil, in the presence of worms, was mainly due to the production of compact casts. The difference in distribution of aggregates between the two treatments was especially significant as soil had been previously sieved at 2.5 mm. The percentages of aggregates of diameter over 2 mm, 0.4–2 mm and less than 0.4 mm were 36.7, 33.8, and 29.6, respectively, in the forest soil before cultivation in the 0–10 cm stratum (Gilot, 1994). Therefore, in 100 days, earthworm activity allowed a macroaggregation of the cultivated soil similar to that of the forest soil, whereas in the absence of earthworms the development of soil macrostructures was much more limited. Water infiltration rate was decreased in the presence of earthworms, probably due to the decreased number of micropores, even though compaction of the ingested soil in casts induced the creation of large pores. *M.*

Table 9
Distribution of soil N and N derived from the labelled litter among fractions (Student's *t*-test, * $P < 0.05$) (with *M. anomala* (MA+) and without *M. anomala* (MA−))

	0–10 cm						10–20 cm					
	Total soil N			Soil N recovered from labelled litter			Total soil N			Soil N recovered from labeled litter		
	MA−	MA+		Ma−	MA+		MA−	MA+		MA−	MA+	
Nnh	24.2	24.6	NS	14.3	19.5	*	27.7	28.2	NS	20.3	19.4	NS
Nhnd	58.5	58.3	NS	78.2	69.4	*	56.7	56.8	NS	72.5	73.3	NS
Nhd	17.4	17.1	NS	7.5	11.1	*	15.5	15.1	NS	7.2	7.3	NS

Nnh, non-hydrolysable nitrogen; Nhnd, hydrolysable distillable nitrogen; Nhd, hydrolysable non-distillable nitrogen.
NS, non-significant difference between MA+ and MA−.

anomala are geophagous endogeic earthworms that feed on humified organic matter. Hence, they do not construct subvertical burrows that link the upper layers to deeper strata; in contrast, the majority of their movement is subhorizontal and they refill with fresh casts most of their galleries.

The aggregation of soil due to earthworm activity may have two undesirable consequences on the soil system—soil compaction and mortality of *M. anomala*. These earthworms are not able to reingest their own casts and when they have ingested a significant proportion of soil, they may starve and die. A possible way to balance these effects would be to introduce, simultaneously to this species, small filiform earthworms of the family Eudrilidae (Blanchart, 1990) that have the ability to break down casts of larger worms into smaller aggregates.

The decrease of *M. anomala* biomass in the experimental units may have been due to excessive soil macroaggregation and rapid decomposition of the organic residues that had been introduced at the beginning of the experiment. In the absence of added organic residues, these worms ingest soil organic matter but growth is slower (Zaidi, 1985; Martin and Lavelle, 1992). Results of the decomposition experiment showed that 90% of organic residues larger than 2 mm had disappeared after 45 days. Earthworms most probably suffered from the shortage of this resource during the latter part of the experiment.

Maize grain yield was increased by 18% in the presence of earthworms. However, difference with the control was significant only at $P = 0.07$. Moreover, grain number and individual weights of grains were increased in the presence of worms. The effects of earthworms were not concentrated on one phase of plant growth but affected plant development during the whole growth cycle (Fleury et al., 1982).

The additional N extracted by maize in enclosures inoculated with earthworms was estimated at 2.4 g per experimental unit, whereas the tissue of dead *M. anomala* (about 30 g liveweight per experimental unit) contained only 0.27 g N. Therefore, dead earthworm organic tissues represented a maximum of 11% of the total surplus exportation of nitrogen in the inoculated units. It has been demonstrated in other studies that the necromass of earthworms has less effect than biomass on plant productivity (Haimi et al., 1992; Graff and Makeschin, 1983). Furthermore, N lost from earthworm biomass may not have benefitted the plant since the worms may have partly escaped the experimental units when conditions became difficult (Martin, 1991b).

Worms improve the use of nitrogen from labelled residues but total nitrogen exportation was not higher. The actual efficiency of organic residue utilisation was 11% in inoculated treatments. This efficiency was much lower than values measured with mineral fertiliser (Ganry, 1990; Balabane and Balesdent, 1992). The amount of nitrogen incorporated in plants is correlated with the quantity of residue decomposed (Müller and Sundman, 1988). Earthworm activity accelerated the release of nutrients from residues to the benefit of plants (Mackay and Kladivko, 1985; Cheshire and Griffiths, 1989). Furthermore, in the presence of worms, N incorporated in soil organic matter was more stable and the proportion of non-hydrolysable nitrogen increased. Worm activity enhanced the storage of residue-N in humified forms in the soil at the expense of fractions which could be easily mobilised. These results might indicate a better synchrony between plant demand and nitrogen availability in soil in the presence of earthworms during the maize growth cycle. Nitrogen derived from labelled litter left in the soil after the crop had been harvested, was potentially less available to plants in inoculated treatments than in control. This N was also less susceptible to leaching because it was in a stable chemical form.

This evidence of a chemical stabilisation of N contrasts with the physical protection of SOM in the compact structure of casts of *M. anomala* hypothesised by Martin (1991a).

Activities of *M. anomala* induced a higher plant production, an effect probably linked to the accelerated decomposition of organic residues introduced before sowing. Nitrogen from this residue had become more readily available and was better used by plants in the presence of earthworms.

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