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EFFECT OF SOIL ORGANIC MATTER QUALITY ON ITS ASSIMILATION BY *MILLSONIA ANOMALA*, A TROPICAL GEOPHAGOUS EARTHWORM

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Summary—Assimilation by *Millsonia anomala* of organic material of decreasing quality (i.e. plant debris at various stages of decomposition, and particle size fractions of soil organic matter) was investigated using cultural and labelling techniques. Assimilation rates were highest with fresh organic matter (undecomposed plant debris or incubated for 2 weeks) and with leaf material rather than root material; this partly results from the high content of watersoluble compounds and the high N availability in fresh organic matter. Earthworm labelling experiments based on ^{13}C showed that after several weeks of decomposition, the nutritive value of plant material rapidly decreases to become equivalent to that of the coarse and fine fractions of the soil organic matter.

INTRODUCTION

As regards the hierarchical model proposed by Lavelle *et al.* (1992), decomposition in soils of the humid tropics is directly under the control of biological factors, such as soil microflora and soil macrofauna. As a consequence, management of soil fertility in the region requires a good knowledge of the diet of organisms feeding on soil.

In most of the humid savannas, soil macrofauna is largely composed by geophagous species (termites and earthworms) which feed on the soil organic matter (Athias *et al.*, 1975; Lavelle *et al.*, 1981). In the wet savannas of Lamto (Ivory Coast), geophagous earthworms represent from 52.5 to 77% of the soil fauna biomass, and annually ingest more than 1000 t soil ha^{-1}, essentially in the upper 20 cm of the soil (Lavelle, 1975). As a result, 15 t ha^{-1} organic matter passes annually through the digestive tracts of earthworms, representing one third of the reserves accumulated in a grass savanna soil and 60% of the organic matter in the first 10 cm of the soil, biotically the most active part of the soil (Lavelle, 1978).

Previous studies showed that the quality, not only the quantity, of soil organic matter determines the growth rate of the worms (Lavelle *et al.*, 1980). In this study we aimed to establish the importance of organic matter quality on its assimilation by *Millsonia anomala*, a geophagous earthworm very common in the wet savannas of Lamto (Ivory Coast). Experiments were carried out to test the ability of *M. anomala* to assimilate various organic materials, from fresh plant debris, composts and physical fractions of the soil organic matter (SOM). A global approach consisted on feeding young earthworms with a soil supplemented with plant material of different origin and evaluate the response of the worms by the way of their total consumption rate, their growth rate and their growth efficiency. The ^{13}C labelling technique provided a complementary approach to study the assimilation of physical fractions of SOM by *M. anomala*.

MATERIAL AND METHODS

This study was carried out at Lamto, Ivory Coast (5°N, 6°W); the climate is characterized by a high mean annual temperature (28°C) and irregular annual rainfall (rainfall averages 1300 mm yr^{-1}, with a dry season from November to March and in August) (Lecordier, 1975). Most soils lie on a granitic bedrock and are classified as "sols ferrugineux tropicaux" (Riou, 1974) or Ferralsol (FAO).

Vegetation is a mosaic of grass and shrub savannas and forest patches (César and Menaut, 1974). Savanna, the most widespread vegetation type, is maintained by regular annual burning.

Savanna soils are very sandy and have a low clay content (from 2 to 10%); as a consequence water retention is low (field capacity from 10 to 13%). These soils have a low C content (from 5 to 12 mg C g^{-1} soil) and the C:N of the 0–10 cm horizon range from 13.9 to 16.2 (Table 1). pH ranges from 5.5 to 6.5.

Rivers are fringed with gallery forests, developed on a loamy soil (field capacity *ca* 20%). The topsoil has a high C content (17.5 mg C g^{-1} soil) and the C:N ratio of the upper 10 cm is *ca* 12 (Table 1). Topsoil pH is 5.2.

Young *M. anomala* were collected in a shrub savanna and raised in laboratory conditions by the method of Lavelle (1975), which allows a measurement of soil consumption rate and the growth rate of the worms.

Table 1. Main characteristics of the experimental soils

	Particle size (μm)	Relative mass (%)	C distribution (mg C g^{-1} soil)	C:N
Shrub savanna (10–25 cm)	Total soil		6.5	15.5
Grass savanna (0–10 cm)	250–2000	44.6	0.84	18.2
	20–250	47.6	2.06	17.6
	0–20	7.8	1.42	13.2
	Total soil		4.32	16.2
Gallery forest (0–10 cm)	250–2000	3.3	1.9	22.2
	20–250	48.4	3.3	14.3
	0–20	48.3	12.3	10.8
	Total soil		17.5	12.6

Three different experimental soils were used: Soil sampled from the 10 to 25 cm layer of the soil profile in a shrub savanna; the soil C content ranges from 6 to 7 mg C g^{-1} soil. Leaves and roots of *Loudetia simplex*, the predominant grass of Lamto grass savannas, were also collected and allowed to decompose under aerobic conditions over 2, 5 or 10 weeks, to obtain plant materials referred as L_0, L_2, L_5, L_{10} for leaves, and R_0, R_2, R_5, R_{10} for roots. 10 mg g^{-1} soil of those organic materials were then added to different soil samples as described by Lavelle *et al.* (1989). For each soil sample, 10 earthworms were raised for 70 days; their soil consumption rate and growth rate were measured every 7 days. Soils were collected in the 0–15 cm layer of the soil profile in a gallery forest and in a grass savanna. C contents of soil were 17.5 and 4.3 mg C g^{-1} soil respectively. Particles of both soils were separated according to their size by physical fractionation. The 250–2000 μm organic fraction (0.8 mg C g^{-1} soil) of two samples of savanna soil was alternatively substituted by the equivalent fraction extracted from the forest soil or by fresh debris of leguminous leaves (*Eriosema* sp.). In a third sample of savanna soil, the 0–20 μm organo-mineral fraction (1.4 mg C g^{-1} soil) was substituted with an equivalent fraction of forest soil. The last experimental soil was obtained adding 1 mg g^{-1} soil of fresh wheat roots to unfractionated savanna soil.

For each soil sample, six earthworms collected in a grass savanna were raised for 25 days. Their growth rate and consumption rate were measured at the end of the experiment.

In that experiment, the introduction of C3 plant material (leguminous, wheat, organic fractions from gallery forest soil) into a soil developed under a C4 vegetation (grass savanna soil) allowed to use ^{13}C as a label to estimate the assimilation of the C3 added material by earthworms as described in Martin *et al.* (1992).

RESULTS

Addition of fresh plant material, except roots of *Loudetia*, improved the growth rate of earthworms and induced a decrease of the consumption rate (Table 2). As a result, yield efficiency defined as:

$$Y = \frac{\text{growth rate}}{\text{amount of C ingested}},$$

was significantly greater in soil supplemented with grass leaves, leguminous leaves and wheat roots, as compared to the control; it was from 1.7 to 2 times that of the control when legume leaves or wheat roots were added to the soil, three times that of the control when *Loudetia* leaves were added (Fig. 1). The increase of yield efficiency did not seem to be correlated with the quantity of N added as fresh plant material. On the other hand, ^{13}C abundance measurements of earthworm tissues pointed out that earthworm fed for 25 days on savanna soil supplemented with legume leaves or wheat roots were significantly

Table 2. Growth rate, consumption rate and yield efficiency of young *M. anomala* fed with savanna soil supplemented with different plant materials (Rel. = relative value)

		N added μg g^{-1}	Growth rate (G) (Δp/p 100 day^{-1})	Rel.	Consumption rate (C) (g soil g^{-1} day^{-1})	Rel.	Yield efficiency (% mg^{-1} C soil)	Rel.
Control			1.9		18.0		8.1	
L. simplex	L_0	72	4.1	2.1	10.7	0.6	16.6	2.0
leaves	L_2	111	4.3	2.3	7.6	0.4	24.1	3.0
	L_5	78	3.9	2.0	12.2	0.7	13.6	1.7
	L_{10}	78	2.3	1.2	12.4	0.7	8.0	1.0
L. simplex	R_0	65	2.3	1.2	13.0	0.7	7.7	0.9
roots	R_2	61	3.1	1.6	14.4	0.8	9.1	1.1
	R_5	80	2.7	1.4	20.2	1.2	5.8	0.7
	R_{10}	57	1.4	0.7	14.4	0.8	4.3	0.5
Control	m		1.3a		26.4a		10.5a	
	σ_{n-1}		0.28		5.4		4.2	
Legume	*m*	52	1.9b	1.5	24.3a	0.9	17.0b	1.6
leaves	σ_{n-1}		0.51		5.0		5.1	
Wheat	*m*	16	2.1b	1.6	20.7b	0.8	21.1b	2.0
roots	σ_{n-1}		0.31		4.0		5.3	
250–2000 μm	*m*		1.5a	1.1	24.3a	0.9	12.6a	1.2
Fract. of SOM	σ_{n-1}		0.39		7.2		3.6	
0–20 μm	*m*		1.7a	1.3	27.1a	1.0	11.2a	1.1
Fract. of SO:M	σ_{n-1}		0.08		6.1		1.7	

For L_x and R_x: x = number of weeks of incubation.
Data from a same column with different letters are significantly different ($P = 0.05$).
m = Average value; σ_{n-1} = standard deviation; 6 replications.

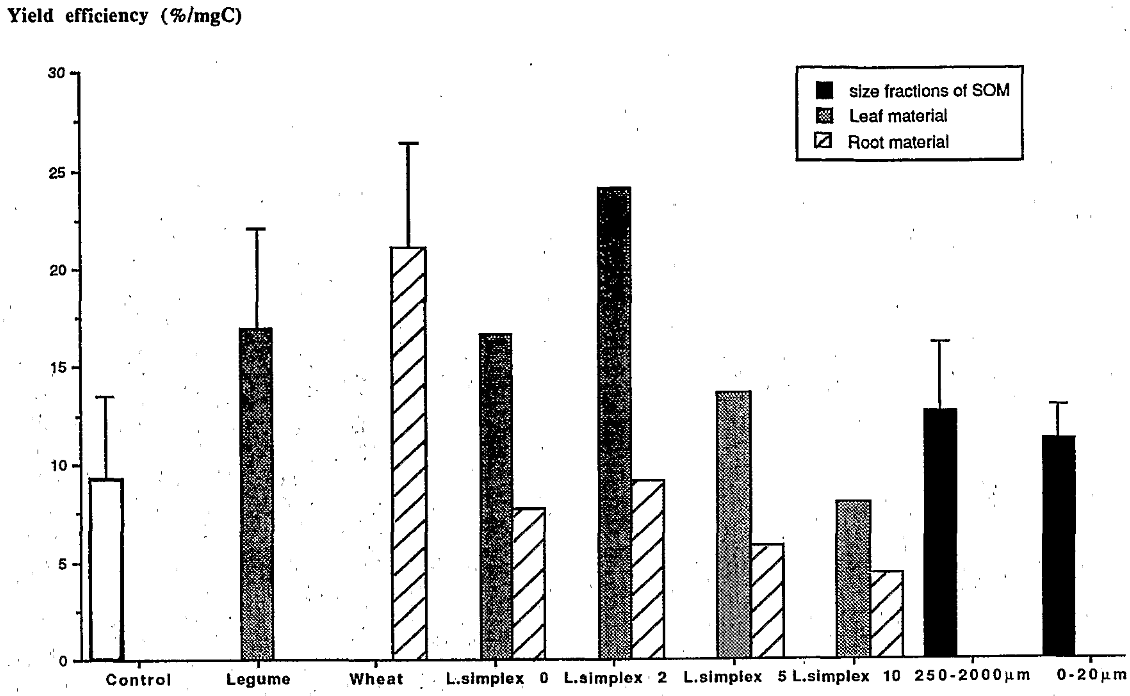

Fig. 1. Yield efficiency of *M. anomala* fed with savanna soil supplemented with different plant materials (L. simplex X = *Loudetia simplex* incubated for X weeks under aerobic conditions, control = savanna soil).

poorer in ^{13}C than earthworms fed for 25 days on savanna soil (Table 3), indicating that the fresh plant debris were assimilated during the experiment. Moreover, the index of assimilation of earthworms fed on soil supplemented with legume leaves was significantly greater than that of earthworms fed on soil supplemented with wheat roots (Table 4).

Addition of *Loudetia* leaves incubated over 2, 5 and 10 weeks resulted in a significant increase of growth rate and yield efficiency. However, the increase of growth rate and yield efficiency was lower with leaf material incubated over a long period (10 weeks); it was similar to that obtained with fresh roots.

Addition of fresh root to the soil had no significant effect on growth rate and yield efficiency. A slight increase of growth rate was obtained only with root material incubated for 2 or 5 weeks; however, the yield efficiency remained quite constant (Table 2).

Substitution of organic fractions in the savanna soil did not induce any significant shift in the growth rate or yield efficiency of earthworms, as compared to individuals fed with the control soil. However, ^{13}C abundance measurements showed that earthworms fed with those soils were significantly labelled (Table 3), indicating that earthworms assimilated the 250–2000 μm and the 0–20 μm fractions of the forest SOM during the experiment; the index of labelling (Table 4) was not significantly different between the coarse organic fractions (250–2000 μm), i.e. young plant residues, and the fine fractions (0–20 μm), consisting mainly of resistant compounds intimately associated with mineral particles (Martin *et al.*, 1990).

DISCUSSION

Fresh plant materials, except *Loudetia* roots, appeared to be good energetic resources that improved the growth rate of young *M. anomala* and decreased their consumption rate. This may be correlated with their high content in easily assimilable organic compounds (water-soluble 1 fraction extracted by Jarrige's Method; Lavelle *et al.*, 1989). On the other

Table 3. $\delta^{13}C$ ratios* (expressed in ‰) of grass savanna soil, forest soil, *M. anomala* collected from a forest soil, and earthworms collected from a grass savanna soil and further fed with savanna soil supplemented with different C3 organic materials

			M. anomala					
		Soil	Control	Legume leaves	Wheat roots	250–2000 μm Org. fract.	0–20 μm Org. fract.
Savanna	m	−12.8	−11.8a	−14.2b	−13.4c	−12.9d	−13.6c
	σ_{n-1}	ND	0.3	0.5	0.3	0.4	0.3
Forest	m	−27.8	−23.5				
	σ_{n-1}	ND	0.2				

$*\delta^{13}C = (^{13}R_{échantillon}/^{13}R_{standard} - 1)\ 1000$, where $^{13}R = {}^{13}C/^{12}C$.
Data from a same line with different letters are significantly different ($P = 0.05$).
(m = Average value, σ_{n-1} = standard deviation).

Table 4. Index of assimilation of different plant materials by *M. anomala*

	I*	
	m	σ_{n-1}
Wheat root	7.6a	1.9
Legume leaves	10.5b	1.1
250–2000 μm Fraction of SOM	3.3c	1.4
0–20 μm Fraction of SOM	2.9c	0.7

*$I = \Delta\delta^{13}C$/g of labelled C ingested.
Data from a same column with different letters are significantly different ($P = 0.05$).
m = Average value; σ_{n-1} = standard deviation; 6 replications.

hand, comparison of growth rates obtained with legume and grass fresh leaves indicated no clear relationship between N content of added material and the increase of growth rate. The increase of growth rate is probably related to the N assimilability of plant material (Abbott and Parker, 1981), that seems to be much higher for legumes than for grasses. A similar result has been reported by Cortez and Hameed (1988) for *Lumbricus terrestris* fed with fresh rye grass or lucerne leaves.

Decomposition of fresh plant material over long periods decreases its nutritive value; after 10 weeks of incubation, the nutritive value may be equivalent to that of the coarse fraction of the soil organic matter (Fig. 1). A similar observation has been reported by Cortez and Hameed (1988); in a laboratory experiment that consisted in feeding *L. terrestris* with rye grass or lucerne leaves incubated for a variable number of weeks, they observed a decrease of growth rates with the length of incubation. This decrease of nutritive value with time of incubation probably results from the loss of easily assimilable organic compounds, very abundant in fresh plant material.

Moreover, the nutritive value of the different organic fractions isolated by physical fractionation was very similar, as indicated by the index of assimilation calculated from ^{13}C labelling experiments. After the loss of easily assimilable compounds, plant residues may thus have a similar nutritive value for young *M. anomala*, irrespective of their size, their age and their relationship with mineral particles.

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