

Soil Biol. Biochem. Vol. 29, No. 3/4, pp. 353–359, 1997 © 1997 Elsevier Science Ltd. All rights reserved Printed in Great Britain PII: S0038-0717(96)00046-6 0038-0717/97 \$17.00+0.00

# EFFECTS OF A TROPICAL GEOPHAGEOUS EARTHWORM, M. ANOMALA (MEGASCOLECIDAE), ON SOIL CHARACTERISTICS AND PRODUCTION OF A YAM CROP IN IVORY COAST

# C. GILOT\*

Laboratoire d'Ecologie des Sols Tropicaux / ORSTOM, 72, route d' Aulnay, 93 143, Bondy cedex, France

## (Accepted 11 January 1996)

Summary—This study was an attempt to validate under field conditions some results of the effects of earthworms on soil organic matter dynamics, obtained under confined circumstances, and on enhanced plant production. Yams were grown in the presence or absence of the tropical endogeic earthworm *Millsonia anomala* (Omodeo and Vaillaud, 1967) for 3 y. Field experiments were conducted in the middle of lvory Coast using experimental plots isolated by PVC sheets. At the beginning of the cropping sequence, earthworm biomass was adjusted to 25 g m<sup>-2</sup>, but as the study progressed the capacity of the soil to sustain populations decreased. By the third year, biomass had decreased to 3 g m<sup>-2</sup>. The presence of worms affected soil structure by increasing the proportion of large aggregates that were mainly ageing casts. In the presence of *M. anomala*, soil C mineralisation decreased by 5% after 3 y, but distribution of C among granulometric fractions of soil organic matter was the same in the two treatments. Yam tuber production was increased by 20%, 0% and 53% at the first, second and third crop, respectively, in presence of *M. anomala*. The earthworms affected both soil and plants but the origin of these effects were unclear © 1997 Elsevier Science Ltd

## INTRODUCTION

Experiments have demonstrated that lumbricid earthworms from temperate areas are capable of stimulating plant growth in grassland and arable land (Syers and Springett, 1984; Lee, 1985). Small-scale experiments, using non-lumbricid tropical geophageous earthworms, have shown similar trends and indicated species-specific responses of plants to earthworm activities (Pashanasi et al., 1992; Spain et al., 1992). Several mechanisms have been suggested by which earthworms can enhance plant growth, e.g. by increased nutrient mineralisation (mainly N) during transit through the earthworm gut and in the casts (Lavelle et al., 1992), and improvement of physical properties resulting in better oxygen and water supplies to the roots (Aina, 1984; E. Blanchart, unpubl. Ph.D thesis, University of Rennes, 1990).

I report the results of an experiment aimed at assessing the effects of the geophageous earthworm, M. anomala, on yam production in a field experiment conducted at Lamto (Ivory Coast). Effects of earthworms on soil structure and soil organic matter dynamics and the production of yam (Dioscorea

Present address: Laboratoire de Bio-Pédologie ORSTOM, BP 13 86, Dakar, Senegal. alata) were monitored for three successive cropping cycles.

#### MATERIAL AND METHODS

## Study site

The study was carried out at the Station d'Ecologie Tropicale de Lamto, Ivory Coast (5°N, 6°W, elevation 105 m) in a shrub savannah representative of the area (César and Menaut, 1974). The climate is characterised by a high mean annual temperature (28.8°C) and irregular annual rainfall (average rainfall 1200 mm y<sup>-1</sup>). The dry season is from November to March and in August (Pagney, 1988).

Soil was a tropical ferruginous soil (ferralsol, FAO-Unesco classification) derived from a granitic parent material. The upper layers (0–40 cm) were characterised by high sand (>75%) and low clay (6 to 10%) contents, low organic content (<1% C) and exchangeable cation contents (Table 1).

At Lamto, soil fauna community is largely dominated by earthworms (Athias *et al.*, 1974), especially geophagous species whose biomass is in the range of 26–43 g fresh wt m<sup>-2</sup> depending on the shrub density (P. Lavelle, unpubl. thesis, 1978). The community of geophageous earthworms is largely dominated by *M. anomala* (Omodeo and Vaillaud, 1967), a large unpigmented mesohumic endogeic species that mainly colo-





	0-1		10-20		20-30		30-40
	a	se	а	se	а	se	
Sand(%) >200 µm	78.1	2.6	77.5	2.4	77.6	3.1	
Loam (%) 2–200 μm	17.0	1.8	14.2	1.1	12.3	3.9	
Clay (%) 0-2 μm	6.0	2.4	8.3	1.4	10.3	1.0	
C (%)	0.85	0.07	0.71	0.07	0.50		0.48
N (%)	0.59	0.04	0.51	0.04	0.44		0.48
C/N	14.5	0.6	13.8	0.8	11.4		10.0
pH (water)	6.75		5.60		5.55		4.75
P assimilable ( $\mu g g^{-1}$ ) (Olsen)	10.3		7.48		7.55		6.31
Ca ech (meg/100)	2.30		1.69		1.31		1.18
Mg ech	1.33		1.00		0.74		0.66
Kech	0.21		0.10		0.09		0.10
Al ech	0.00		0.00		0.00		0.02
CEC	4.37		3.09		2.75		2.77
S	3.91		2.82		2.19		1.97

Table 1. Texture and chemical characteristics of the savannah soil down to 40 cm (a: average; se: standard error)

nises the upper 20 cm of the soil (Lavelle, 1981). Biomass of *M. anomala* populations ranges from 7 to 40 g m<sup>-2</sup> and the largest adults may be 17 cm long and weigh 5 g fresh wt.

# Experimental design

The experiment was set in a plot of a shrub savannah. Twenty circular microplots  $0.72 \text{ m}^2$  each were isolated by thick PVC sheets inserted down to 45 cm, with a rim of 10 cm above the surface. Two treatments were considered, with *M. anomala* (MA+), without *M. anomala* (MA-); *Millsonia anomala* were introduced in half of the experimental units at a biomass of 25 g fresh wt m<sup>-2</sup> in May 1990. The experiment comprised 10 replicates for each treatment and ran for 3 y, from April 1990 to December 1992. Each experimental unit contains one yam plant. Experimental units were surrounded with non-experimental plants.

In April 1990, a carbamate (carbofuran 2,3-dihydro-2,2-dimethyl 1,7-benzofuranyl methylcarbamate; 0.41 g m<sup>-2</sup> active substrate) was applied in each unit to kill the native worms. Yams (*Dioscorea alata* cultivar Hawai) were planted for the first time in May 1990 in mound cultivation; plants were staked only the third year with stakes of 2 m heigh. Measurements of plant and soil parameters were done after each cropping period.

The fresh and oven-dry (105°C) production of tubers and above ground production were measured separately. The all soil of each experimental unit was handsorted to 30 cm depth to recover the earthworms. Worms were identified at the species level (except for Eudrilidae which can only be distinguished at the adult stage after fixation in formalin), counted and weighed alive. Some samples were preserved in 4% formalin before identification (weight in formalin is approximately 75% of live weight). The worms sorted were not reintroduced in experimental units. New *M. anomala* were reintroduced before each cultivation in the (MA+) treatment (Table 2).

تهوتان الله المن المحافظ

The mounds were  $\pm 20$  cm high. They were made with 0–10 cm depth soil and they are considered as 0– 10 cm depth soil. Soil samples were taken in the mound (+10–0 cm), and in the 0–10 cm stratum, mixed together, and in the 10–20 cm depth stratum in half of the experimental units (5 replicates per treatment). The soil was air dried, homogenised, and sieved (2 mm) to remove live roots.

Soil organic matter was separated into particle-size fractions using the Feller method (Feller, 1979). Forty g of soil was mixed with 200 ml water and disaggregated by shaking (by hand) and applying low energy sonication (80 W; 30 min long) until complete dispersion of the soil aggregates was obtained. Fractions were separated by wet sieving at 250, 100, 50 and 20 µm mesh sizes. Sand and organic fragments are found in fractions larger than 20 µm; silt and clay-associated organic matter and soluble extracts are found in the 0-20 µm fraction. Separation of the 0-2 µm and 2-20 µm was done by sedimentation using Stokes law. One replicate per treatment was done on soils sampled in April 1990 (before cultivation) and in December 1992. Soil samples were obtained by mixing soil from the five replicates per treatment.

Soil aggregation was evaluated after the third crop in 5 replicates. The soil sampled for this analyse has been sorted the previous year; so it was disturbed and crumbled. Monoliths  $(20 \times 20 \times 20 \text{ cm})$  were separated in two layers (+10-0 and 0-10 cm) broken into large fragments (ca. 800 cm<sup>3</sup>) and air-dried to a moisture content of 5-6% dry wt (pF  $\approx$  4). Aggregates were

Table 2. Biomass (g fresh wt  $m^{-2}$ ) of *M. amomala* introduced before each cropping period in the microplots "MA + "

date	worm biomass
Apr 90	25
Apr 91	28.5
Apr 92	30



Fig. 1. Biomass of *M. anomala* in the experimental units at the three cropping periods (month/year). \*P < 0.05 (differences between treatments at each date, t-test).

separated by dropping the air dried fragments from a constant height of 1.5 m onto a hard surface. They were further air dried and sieved on grids with respective mesh sizes of 10 mm, 6.3 mm, 5 mm, 2 mm, 1 mm, 630  $\mu$ m, 500  $\mu$ m, 400  $\mu$ m, 315  $\mu$ m, 250  $\mu$ m. Weights of respective fractions were evaluated (Blanchart *et al.*, 1990). Then three main classes were retained: >2 mm, 0.4–2 mm, <0.4 mm.

Statistical analysis were performed with the software Statview.

## RESULTS

#### Earthworm populations

The elimination of earthworms was not complete (Fig. 1 and Fig. 2). Four species were found in the experimental units after the first crop i.e. *M. anomala, Dichogaster agilis,* and two species of Eudrilidae (*Chuniochilus zielae and Stuhlmenia porifera*). The biomass of *D. agilis* and Eudrilidae did not differ significantly in the MA+ and MA- treatments, and was very low in comparison with the biomass of *M. anomala* (Fig. 1 and Fig. 2). Hand-sorting of the worms after each crop enabled the elimination of undesired earthworms. Although the biomass of *M. anomala* was

significantly greater in the MA+ treatment than in MA- (Fig. 1), values measured at each harvest were always lower than the introduced biomass. Only 4.2 and 2.6 g m<sup>-2</sup> were recovered after the second and the third cultivation periods, respectively. This may be partly explained by the date of the sampling (December or January) i.e. at the beginning of the dry season when a large proportion of worms was quiescent. The high percentage of juvenile worms recovered indicated that reproduction had occurred (36% and 86% at the second and third harvests respectively).

The comparison of the earthworm population in the experimental units and in the savannah was performed after the third cultivation period in December 1992 (Table 3). Earthworms were sampled in the savannah using the TSBF methodology (Anderson and Ingram, 1992) in 12 monoliths of  $25 \times 25 \times 40$  cm. The bioof mesohumic endogeic species mass (M. anomala + Dichogaster terrae-nigrae) was three times higher in the savannah than in the MA+ units. Accordingly, the sampling period is not the only reason for the low density recovered, hence the conditions induced by the vam mound-cultivation may be unfavourable to the worms.

#### Soil structure

The size distribution of aggregates observed in the mound (+10-0 cm) and in the 0–10 cm strata differed among treatments (Table 4). The percentage of small (<0.4 mm) and intermediate (2–0.4 mm) aggregates was lower in treatment MA+ than in treatment MA – , whereas the large aggregates were more abundant in the treatment MA + . Size distribution of aggregates in soil inoculated with *M. anomala* was similar to that of the original soil after the third crop.

### Soil organic matter

C content of the soil decreased by 30% after 3 y of cultivation in the 0–10 cm strata and in the 10–20 cm strata, irrespective of the treatment (Fig. 3). The changes in the N content were less important. Moreover, the C and N contents were somewhat higher in the 0–10 cm strata in December 1992 in MA + treatment than in MA-- treatments; the differ-



Fig. 2. Biomass of Dichogaster sp (A) and Eudrilidae (B) in the experimental units at the three cropping periods (month/year).

Table 3. Biomass (g m<sup>-2</sup>) of earthworms in the experimental units and in the nearby savannah in December 1992. m: mean; se: standard error

		M.anomala	Eudrilidae	D. agilis	D. terrae nigra	Total
MA-	m	0.00	0.02	0.11	0.00	0.1
	se	0.00	0.01	0.05	0.00	0.0
MA+	m	2.58	0.00	0.25	0.00	2.8
	se	1.04	0.00	0.14	0.00	1.0
Savannah	m	11.17	5.86	0.52	7.84	26.3
	se	1.33	1.03	1.62	2.32	0.9

ence is significant for P < 0.10. Particle size fractionation of the organic matter did not show differences in the distribution of organic carbon among the different size classes between treatments MA + and MA– (Fig. 4). During the 3 y of cultivation, organic matter <2 µm had decreased in particular. Organic matter inputs (surface application of legume residues before cultivation, *Erythrosema sp*, 2.5 t ha<sup>-1</sup>, during the first 2 y and peanut residues the third year) were apparently not sufficient to compensate for the mineralisation of soil organic matter.

# Production

Mean tuber production was similar in the first 2 y, at ca. 30 t fresh wt.  $ha^{-1}$  (mean tuber weight: 2.1 kg). Very low yields were obtained in the third year when the mean weight of tubers had dropped to 350 g.

Tuber production was 20% higher in the presence of *M. anomala* in the first year (Table 5). No difference in yield was observed the second year. In the third year, the difference between the yam tuber production in treatment MA+ and MA- was 53%. However because of the huge heterogeneity of plant production, the significance of the difference was low (P < 0.10). The production of the above-ground parts was also generally increased in the presence of worms, but not significantly.

### DISCUSSION

Populations of *M. anomala* could survive in the yam crop although with a much lower biomass than in the surrounding savannah. Microclimatic conditions may be responsible for the mortality of earthworms inside the experimental units. Worms can not escape adverse conditions as they do in savannah (S. Martin, unpubl. Ph.D thesis, University of Paris VI, 1991). The lack of soil cover will have induced a rapid increase of soil temperature. Deposition of plant residues seems not to have been effective enough to replace plant cover when plants were small, because residues were rapidly exported out of the experimental units by termites. Also, *M. anomala* may have been affected by the decrease of the less humified organic matter which is their food resource (Kale and Krishnamoorthy, 1981; Baker *et al.*, 1992)

Earthworms significantly affected soil aggregation during the cultivation periods. *M. anomala* are known to ingest huge amounts of soil every day, 5 g g<sup>-1</sup> and 30 g soil g<sup>-1</sup> fresh wt for adult and juvenile worms respectively (Lavelle, *loc. cit.*). Natural populations may annually ingest up to 500 Mg ha<sup>-1</sup> resulting in the accumulation of larges casts that are the component elements of the macroaggregate structure in natural savannah soil. In our experiment, the earthworms increased the percentage of large aggregates. However, the huge differences observed between the two treatments was partly an artefact of the experimental design; hence, the soil was fragmented every year for the sampling of the worms.

Mineralisation of soil organic matter was slower in the presence of earthworms than when they were absent. The same phenomenon has been observed under laboratory conditions with this earthworm species. Decomposition processes are slowed down in the order of years in ageing casts (Martin, 1991). Since organic matter is protected in the compact structure of casts, the bonds between organic and mineral components may further be strengthened by organic products secreted through the gut and when the casts age (Shipitalo and Protz, 1989). But on a shorter time scale, which was not examined here, the decomposition process is drastically accelerated during gut transit through fragmentation and with a flush of

Table 4. Percent distribution of aggregates in three classes in two strata : mound (+10-0 cm) and 0-10 cm (Fisher test). Values within row followed by a different letter are significantly different at P < 0.05 (values of the savannah were not compared to those of the treatments because the soil of the savannah was undisturbed whereas the soil of the treatment was disturbed)

		savannah	MA+	MA-
< 0.4 mm	mound		22.4 a	32.1 b
	0–10 cm	25.1	27.2 a	31.2 b
0.4–2 mm	mound		24.1 a	38.1 b
	0–10 cm	25.7	30.5 a	38.8 b
>2 mm	mound		53.5 a	29.8 b
	0–10 cm	49.2	42.3 a	30.0 b



Fig. 3. Carbon and nitrogen contents of the 0–10 cm and 10–20 cm. \*Significant differences (differences between treatments at each date, t-test, P < 0.10).

mineralisation. In fresh casts, large amounts of nutrients are released (Sharpley *et al.*, 1979; Mackey *et al.*, 1982; Lavelle *et al.*, 1992). Hence, *M. anomala* has different effects on soil organic mater, depending on the time scale of observation. However, for the duration of the experiment, the presence of worms appeared to lead to a protection of organic matter.

Cultivation induced a 60% decrease of the C content of the coarser organic material (>20  $\mu$ m) in 3 y irrespective of the presence of earthworms; but no difference was observed in the repartition of the organic C among granulometric fraction in the two treatments. It is generally assumed that the size of the



Fig. 4. Carbon repartition (%) in three granulometric classes: 0-2 μm, 2-20 μm and 20-2000 μm in April 1990 (savannah) and in December 1992 (Treatment MA- and MA+).

particles is linked to their age (the coarser particules are the less humified) (Tiessen and Stewart, 1983). Hence, the input of plant residues was apparently not sufficiant to compensate for the fragmentation of the coarse particule. Protection of organic matter (5%; Fig. 3) was not specific of any particular particule-size fractions. In another experiment, we found that when crop residues were incorporated into the soil, the mineralisation of the coarser fraction was higher in the presence of *M. anomala* than in their absence (C. Gilot, unpubl. Ph.D. thesis, INA-PG, 1994). This demonstrated that ingestion of soil by these earthworms resulted in the fragmentation of the coarser organic soil debris.

The production of yam tubers was increased in the presence of earthworms during the first and third year of the experiment, by 20% and 53% respectively. No effect was measured during the second year. Yields of the first 2 y were about as high as yields obtained in central Ivory Coast on savannah soils (Thouvenel and Dumont, 1990) and in Sierra-Leone (Envi, 1972). The very low production of the third year could not be explained by unfavourable climatic conditions during the year nor by attacks of pathogens (Gilot, loc. cit.). Yam is not suitable for continuous cultivation and such yield losses are frequently observed (Gigou, 1987). Earthworm activities only affected the amount of dry matter produced; N contents of tubers (ca. 0.95%, on average for the 3 y) were not significantly affected (Gilot, loc. cit.).

year	MA	MA+	increase in presence of worms (%)	Р
90	475.3	571.7		< 0.05
91	514.5	510.4	-1	>0.10
92	82.2	125.7	53	< 0.10
90	51.5	68.9	33	< 0.10
91	33.5	41.6	24	>0.10
91	19.2	25	30	>0.10

Table 5. Yam tuber production (g plant<sup>-1</sup> dry wt), aerial parts (g plant<sup>-1</sup> dry wt) (t-test)

During the first cropping cycle, climatic conditions were unfavourable. We measured a hydric deficit in 5 successive periods (70 to 120 days after planting). Soil moisture was significantly higher in the presence of earthworms after the second and third cropping period (not determined in first cropping period). The effect of earthworms may be linked to the hydric conditions during cultivation. On the other hand, earthworm biomass was still high after the first cultivation and earthworms certainly have been active for a longer period than the following years.

Soil organic matter content was considerably decreased during the experiment. In the absence of any input of fertilizer, plant demand may have been greater than the actual available pool of assimilable nutrients. In the presence of earthworms, nutrient mineralisation may have been higher resulting in a higher production.

The ingestion of soil by M. anomala induced great modifications of the soil. The soil was more macroaggregated in the presence of earthworms. This is especially important in the mound where, in the absence of earthworms the soil would have kept a particular structure during the whole cultivation period and would have been more sensitive to soil erosion especially when violent tropical storms occur. Soil aggregation allowed the protection of the soil organic matter. The protection of soil organic C in the presence of M. anomala is limited (5%) at the time scale of the experiment but it may be higher for a longer period. Yam growth was improved in the presence of the geophageous earthworm M. anomala; the origin of the effect on plant production has not been clearly identified, but we assume that it may be linked to earthworms improving soil hydrologic conditions and nutrient availability.

Acknowledgements—I would like to thank Dr P. Lavelle for comments on earlier draft of the paper, Dr C. Feller for his contribution to this work, M. Vuattoux and everyone at the ecological station of Lamto.

# REFERENCES

- Aina P.O. (1984) Contribution of earthworms to porosity and water infiltration in a tropical soil under forest and longterm cultivation. *Pedobiologia* **26**, 131-136.
- Anderson J. M. and Ingram J. S. I. (Eds) (1992) A Handbook of Methods. Tropical Soil Biology and Fertility C.A.B, Oxford.

- Athias F., Josens G. and Lavelle P. (1974) Le peuplement animal des sols de la savane de Lamto. In *Analyse d'un écosytème tropical humide: la savane de Lamto* pp. 45–53. Publication du Laboratoire de Zoologie de l'ENS.
- Baker G., Buckerfield J., Grey-Gardner R., Merry R. and Doube B. (1992) The abundance and diversity of earthworms in pasture soils in the Fleurieu Peninsula South Australia. Soil Biology & Biochemistry 24, 1389-1395.
- Blanchart E., Lavelle P. and Spain A. (1990) Effects of biomass and size of *Millsonia anomala* (Oligochaeta: Acanthodrilidae) on particle aggregation in a tropical soil in the presence of *Panicum maximum*. *Biology and Fertility* of Soils 10, 113-120.
- César J. and Menaut J. C. (1974) Le peuplement végétal de la savane de Lamto. In Analyse d'un écosystème tropical humide: la savane de Lamto, pp. 1–161. Publication du Laboratoire de Zoologie de l'ENS Paris.
- Enyi B.A.C. (1972) Effect of staking, nitrogen and potassium on growth and development in lesser yams: Dioscorea esculenta. Annals of Applied Biology 72, 211-219.
- Feller C. (1979) Une méthode de fractionnement granulométrique de la matière organique des sols: application aux sols tropicaux à texture grossière, très pauvres en humus. *Cahiers O.R.S.T.O.M., série Pédologie* XVII, 339-346.
- Gigou J. (1987) L'adaptation des cultures dans le centre de la Côte d'Ivoire. L'Agronomie Tropicale 42, 1–11.
- Kale R. D. and Krishnamoorthy R. V. (1981) What affects the abundance and diversity of earthworms in soils? *Proceedings of Indian Academy of Sciences — Animal Science* 90, 117–121.
- Lavelle P. (1981) Stratégies de reproduction chez les vers de terre. Acta Æcologica 2, 117-133.
- Lavelle P., Melendez G., Pashanasi B. and Schaefer R. (1992) Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex Corethurus* (glossoscolecidae). *Biology and Fertility of Soils* 14, 49–53.
- Lee K. E. (1985) Earthworms: their Ecology and Relationships with Soils and Land Use. Academic Press, New York.
- Mackey A.D., Springett J.A. and Syers J.K. (1982) Origin of the effect of earthworms on the availability of phosphorus in a phosphate rock. Soil Biology & Biochemistry 15, 63– 73.
- Martin A. (1991) Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biology and Fertility of Soils* 11, 234–238.
- Pagney P. (1988) Le climat de Lamto (Côte d'Ivoire). In Le climat de la savane de Lamto (Côte d'Ivoire) et sa place dans les climats de l'ouest africain (Lamotte M. and Tireford J. L., Eds), pp. 31-79. Travaux des chercheurs de Lamto (RCI).
- Pashanasi B., Melendez G., Szott L. and Lavelle P. (1992) Effect of inoculation with the endogeic earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on N availability, soil microbial biomass and the growth of three tropical fruit tree seedlings in a pot experiment. *Soil Biology* & *Biochemistry* 24, 1655–1659.

- Sharpley A.N., Syers J.K. and Springett J.A. (1979) Effect of surface-casting earthworms on the transport of phosphorus and nitrogen in surface runoff from pasture. *Soil Biology & Biochemistry* 11, 459–462.
- Shipitalo M.J. and Protz R. (1989) Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* **45**, 357–374.
- Spain A.V., Lavelle P. and Mariotti A. (1992) Stimulation of plant growth by tropical earthworms. Soil Biology & Biochemistry 24, 1629–1633.

Ŷ

Syers J.K. and Springett J.A. (1984) Earthworms and soil fertility. *Plant and Soil* 76, 93-104.

- Thouvenel J.C. and Dumont R. (1990) Perte de rendement de l'igname infectée par le virus de la mosaïque en Côte d'Ivoire. L'Agronomie tropicale **45**, 125–129.
- Tiessen H. and Stewart J.W.B. (1983) Particle-size fractions and their use in studies of soil organic matter: II. Cultivation effects on organic matter composition in size fractions. Soil Science Society of Americal Journal 47, 509-514.