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Phosphorus transformations in a ferralsol through ingestion by *Pontoscolex corethrurus*, a geophagous earthworm

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Abstract – This paper analyses the transformations that result in increased inorganic phosphorus (Pi) content in a ferralsol after transit through the gut of the earthworm *Pontoscolex corethrurus.* Total, inorganic and organic P contents were measured in bulk samples of dry soil, incubated and non-ingested soil and surface casts, and in chemical extracts on samples previously separated into three particle-size fractions (> 20, 2–20 and < 2 µm). The total P content was the same in control, non-ingested soil and casts but remoistening and transit through the earthworm gut decreased organic P and increased inorganic P contents. Clay content in surface casts (19.7 %) was significantly higher than in the control soil (9.1 %). Phosphate content significantly increased in the $NaHCO_3$ extract from 3.17 in non-ingested soil to 5.04 µg $Pi \cdot g^{-1}$ soil in casts; the same trend was observed in NaOH extract with 27.4 in non-ingested soil and 45.8 µg $Pi \cdot g^{-1}$ soil in casts. Phosphate in casts was mostly concentrated in the finest fractions (0–2 µm) with 83 % of extracted phosphate, opposed to 61 % in non-ingested soil. These changes resulted from a combination of selective ingestion of small particles and partial mineralisation of organic P. © Elsevier, Paris

Surface casts / *Pontoscolex corethrurus* / phosphate / particle-size fractions / $NaHCO_3$ extract / NaOH extract

Résumé – Transformations du phosphore d'un ferralsol suite à l'ingestion par le ver géophage *Pontoscolex corethrurus*. Ce travail analyse les transformations qui conduisent à augmenter le contenu en phosphore inorganique (Pi) assimilable du sol suite à l'ingestion d'un ferralsol par le ver géophage *Pontoscolex corethrurus*. Le contenu en phosphore total, inorganique et organique d'échantillons de sol témoin, de sol non-ingéré mais incubé et de déjections de surface a été mesuré. Le phosphore extractible par $NaHCO_3$ et NaOH a été dosé dans des échantillons ayant préalablement subi un fractionnement granulométrique (> 20, 2–20 et < 2 µm). La teneur en phosphore total est la même dans le sol témoin, le sol non-ingéré et les déjections ; la réhumectation du sol et l'ingestion du sol par le ver diminuent la teneur en phosphore organique et augmentent la teneur en phosphore inorganique. La teneur en argile des déjections (19,7 %) est significativement supérieure à celle de l'échantillon témoin (9,1 %). Les turricules ont une teneur en phosphore inorganique extractible par $NaHCO_3$ significativement supérieure à celle du sol non-ingéré (5,04 µg $Pi \cdot g^{-1}$ sol contre 3,17). La même tendance est observée dans l'extrait NaOH (45,8 µg $Pi \cdot g^{-1}$ sol dans les déjections contre 27,4 dans le sol non-ingéré). Les phosphates dans les déjections sont essentiellement concentrés dans les fractions granulométriques fines (0–2 µm) (8,3 % des phosphates extraits contre 61 % pour le sol non-ingéré). Ces modifications résultent de l'ingestion sélective par le ver de particules fines et de la minéralisation partielle du phosphore organique. © Elsevier, Paris

Déjections de surface / *Pontoscolex corethrurus* / phosphate / fractions granulométriques / extrait $NaHCO_3$ / extrait NaOH

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1. INTRODUCTION

Earthworms have diverse functions in soil processes and may affect phosphorus cycling. James [12] observed a significant increase in phosphate content in casts compared to the surface soil layer in a tallgrass prairie. Mackay et al. [20] demonstrated that burrowing and casting earthworms activities indirectly increase the phosphorus bioavailability of a phosphate rock by a redistribution and intimate contact of the fertiliser with the soil. Sharpley and Syers [29] evaluated the contribution of epigeic earthworm casting activity as a potential source of particulate and dissolved phosphorus to runoff waters in pasture watersheds. The species studied by Sharpley and Syers [29, 30] consumed plant materials derived from the litter layer of grassland soils. In tropical soils, higher contents of phosphate are observed in casts than in the corresponding surface soil layer [14, 23, 31]. The contribution of geophagous earthworms to phosphate recycling in soil surface layer could be important [11].

Pontoscolex corethrurus Müller is a peregrine species with a high adaptative capacity, especially after slash and burn under herbaceous vegetation in humid tropics [17]. López-Hernández et al. [19] fed this worm with two phosphorus-sorption contrasting soils. They observed that exchangeable phosphate was more abundant in casts than in the control soil. A significant increase of exchangeable phosphate was also observed in the casts of the same species fed with a ferralsol [8]. This increase resulted from the mixing of soil and plant materials during the gut transit. The present study was designed to identify changes in P cycling occurring during gut transit.

Adult *Pontoscolex corethrurus* were cultured in an homogenised ferralsol in laboratory conditions. Particle-size analyses of surface casts, dry control soil and non-ingested soil were carried out to check for the selective ingestion of soil particles of a given size. Chemical transformations were characterised by a chemical fractionation of phosphorus labile forms in the different classes of particle-size fractions separated.

2. MATERIALS AND METHODS

2.1. Earthworms culture

The control soil was taken from the upper 10 cm of a ferralsol supporting a 18-year-old secondary forest (Yurimaguas, Peruvian Amazonia) (*table I*). This silty sand topsoil is acidic, with low exchange capacity and base saturation and its total phosphorus content is similar to other ferralsols [24]. Ten soil samples of 1 kg were taken at random, mixed, air-dried and thoroughly homogenised. Earthworms of the species *Pontoscolex corethrurus* (Glossoscolecidae) were taken from a nearby pasture and left for 2 d in the experimental soil, previously moistened, to empty their guts of the pasture soil that they had ingested.

Table I. Physico-chemical characteristics of the experimental soil.

Sand ($g{\cdot}kg^{-1}$)	677
Silt	230
Clay	91
Water-holding capacity ($g{\cdot}g^{-1}$)	0.39
pH w	4.4
pH KCl	3.6
CEC ($cmol_c{\cdot}kg^{-1}$)	4.82
Ca^{++}	0.37
Mg^{++}	0.23
K^+	0.10
Na^+	0.02
Al^{+++}	4.15
Cations	5.30
C ($g{\cdot}kg^{-1}$)	20.8
C/N	13.9
Total P ($mg{\cdot}kg^{-1}$)	190.7
Organic P	155.6
Inorganic P	35.1
Pw ($mg{\cdot}L^{-1}$)	0.04

They were further kept in five boxes filled with 0.7 kg experimental soil which had been previously sieved through a 4-mm mesh after coarse roots had been excluded, and moistened at 0.31 $g{\cdot}g^{-1}$ soil (i.e. 80 % water-holding capacity). Soil bulk density was adjusted to 1.11 $g{\cdot}dm^{-3}$ to stimulate the production of surface casts. Each of the five culture boxes contained 20–25 worms and the biomass per box was 12.71 ± 0.08 g. Temperature was kept at 28 °C, and the soil water content was adjusted daily. Casts deposited at the surface of the soil were collected every 12 h, stored at 4 °C until the analyses were performed. After a week, the worms were removed from the boxes. The non-ingested soil was separated from casts deposited in the soil as described by Lavelle et al. [17], and stored for analysis. Daily surface casts production was from 20 to 36 g per day per box. During 7.5 d, the total deposit of fresh casts was 80 to 133.5 g per box.

2.2. Particle-size fractionation

Analyses were performed on control soil, non-ingested soil and surface casts. Samples were shaken (50 rpm) for 17 h in water (soil/water ratio = 1/10). Particle-size fractionation was then performed by sieving through 200, 50 and 20-μm mesh size. Fine-silt fraction (F 2–20 μm) was separated from clay fraction (F 0–2 μm) by sedimentation. The plant residue fraction (light fraction Fl > 200 μm) was separated by densimetry in water. Three replicates of the control soil, non-ingested soil and surface casts were fractionated. The mass balances ranged from 97.2 to 101.2 %. After calculating mass balances, fractions larger than 20 μm, except the light fraction Fl > 200 μm, were grouped for chemical determinations.

2.3. Particle-size analysis

Total Na-resin dispersion-disaggregation was performed on control and surface casts samples as described by Rouiller et al. [25], Bartoli et al. [3] and Feller et al. [10].

The comparison between particle-size analysis and fractionation results allowed the quantification of a possible selection of particle size by the worms.

2.4. Carbon, nitrogen and phosphorus

Analyses were performed on control, non-ingested soil, surface casts and particle-size fractions. Total C and N contents were obtained by dry combustion using an ANA 1500 Carlo Erba analyser. Total P (Pt) was determined by colorimetric method [9] after combustion at 550 °C and digestion in concentrated nitric acid of 2-g samples [16]. Total organic P (Po) was measured according to Saunders and Williams [28]. Total inorganic P (Pi) was calculated as the difference between Pt and Po.

2.5. $NaHCO_3$ and NaOH P fractions

The 20–2 000, 2–20 and 0–2 μm particle-size fractions were subjected to sequential extraction of phosphorus in three replicates. Extractants were chosen to remove inorganic and organic P. First labile Pi and Po sorbed on surfaces, plus a small amount of microbial P, were removed with a 0.5 M $NaHCO_3$ extraction [6]. A 1-g sample was shaken with 30 mL of a 0.5 M sodium bicarbonate solution for 17 h. The suspension was centrifuged, filtered and acidified with concentrated H_2SO_4. The $NaHCO_3$ extraction was followed by a 0.1 M NaOH extraction with the same procedure to remove Pi and Po compounds held more strongly by chemisorption to iron and aluminium components of soil surfaces [22, 26]. Phosphate in the extracts were colorimetrically determined [13]. Total P contents in $NaHCO_3$ and NaOH extracts were measured after nitric oxidation. Extractable organic P contents were calculated as the difference between total P and phosphate contents in the extracts.

2.6. Statistics

For chemical analysis, error variances were estimated from the measured data. For determination of C and N contents we assumed standard deviations of 2 %. In *table V*, total and inorganic P contents varied with maximum standard deviation of 13 % for the 2–20 and 20–2000 μm fractions and 5 % for the finest fraction.

t-Tests were performed and values were considered as different when probability was smaller than 5 %.

3. RESULTS

3.1. Phosphorus and carbon contents in bulk samples

No significant difference was observed in total phosphorus contents of the control, non-ingested soil and casts (*table II*). Regarding organic and inorganic P contents and C and N contents, there were no significant difference between control and non-ingested soil, nor between non-ingested soil and surface casts. Differences were significant only between casts and control soil. Organic P content was lower and inorganic P was higher in casts than in the control.

Table II. Phosphorus (μg $P \cdot g^{-1}$ soil), carbon and nitrogen ($g \cdot 100\ g^{-1}$ soil) contents in control, non-ingested soils and fresh surface casts.

	Control	Non-ingested soil	Surface casts
Phosphorus (μg $P \cdot g^{-1}$)			
Total	190.7 a	193.7 a	192.9 a
Organic	155.6 a	137.1 ab	131.6 b
Inorganic	35.1	56.8	61.3
Carbon ($g \cdot 100\ g^{-1}$)	2.08 a	2.23 ab	2.31 b
Nitrogen ($g \cdot 100\ g^{-1}$)	0.14 a	0.17 ab	0.18 b
C/N	14.89 a	13.18 ab	12.8 b

Data within the same analysis with different letters significantly differ at $P < 5\ \%$.

3.2. Mass particle-size distribution

The particle-size analysis of the control soil and the casts showed significant differences in the 50–200 and 0–2 μm fractions with, respectively, a decrease and an increase in surface casts compared to control (*table III*).

The dispersion of soil and cast samples before particle-size fractionation yielded fractions containing stable aggregates after 17 h of shaking in water. The gut transit significantly reduced the respective amounts of the 200–2000 and 50–200 μm size particles, had no effect on 20–50 μm fraction and increased the proportion of the finest fractions. The levels of aggregation can be calculated as the difference between the values obtained by the maximum dispersion (particle-size analysis) and the 17-h agitation in water (particle-size fractionation). Aggregates larger than 200 μm represented 18.9 % of the control soil mass and only 7.7 % of the surface casts.

3.3. Organic matter and total P distribution in particle-size fractions

The respective carbon contents (mg $C \cdot g^{-1}$ soil) in the Fl > 200 (plant residue fraction), F > 20 and 0–2 μm fractions decreased from control to non-ingested soil

Table III. Mass particle-size distribution obtained in the particle-size analysis (max. dispersion) and particle-size fractionation (17 h shaking) of the control soil and surface casts (g·100 g^{-1}).

Fractions µm	Particle-size analysis (g·100 g^{-1})		Particle-size fractionation (g 100 g^{-1})	
	Control	Casts	Control	Casts
200–2 000	12.2	14.8	31.1 a	22.5 b
50–200	55.5 c	43.2 d	46.9 a	39.8 b
20–50	11.4	11.1	9.8	9.7
2–20	11.6	11.7	9.2 a	13.0 b
0–2	9.1 c	19.7 d	4.2 a	12.9 b
	99.8	100.5	101.2	97.9

Data within a same analysis and a same particle-size fraction with different letters significantly differ at $P < 5$ %.

and surface casts, and increased in the 2–20 µm fractions ($P < 5$ %). No significant difference between control and casts was observed in the value of the C/N ratio of the 2–20 µm fraction. The C/N ratios were significantly different for the other fractions of control, non-ingested soil and casts (*table IV*). The C/N ratios increased following the sequence: control soil < non-ingested soil < surface casts.

In surface casts, total P contents (µg P·g^{-1} soil) in fractions Fl > 200 and F > 20 µm were significantly lower than in non-ingested soil and control, while in the finest fractions, the opposite trend was observed.

3.4. Extractability of P

The extracted Pt represented 36.6 % of the total Pt in control soil with 4.5 % in $NaHCO_3$ extract and 32.1 % in NaOH extract (*table V*). The proportion was 42.4 % in non-ingested soil, mainly in the NaOH extract (35.3 % of Pt). The chemical extraction operated on surface casts yielded 44.5 % of total Pt, with 6.3% in $NaHCO_3$ extract and 38.2 % in NaOH extract.

A large proportion of inorganic P contents in bulk samples was extracted: 94.8 % in control soil and 83 % in surface casts versus only 53.8 % in the non-ingested soil (*table V*).

Extracted organic phosphorus represented from 25.3 % to 37.7 % of total organic P (*table V*).

3.5. Distribution of P in chemical and particle-size fractions

NaOH extracted more phosphorus than $NaHCO_3$ (*table V*).

Total P contents extracted by $NaHCO_3$ solution were similar in non-ingested soil and casts, and greater than in control soil (*table V*). No significant difference was observed in inorganic P extracted from control and casts but the Pi content increased from non-ingested soil to casts with respectively 3.17 and 5.04 µg Pi·g^{-1} soil.

Control, non-ingested soil and casts presented similar extracted total P contents in the NaOH extracts

Table IV. Mass, total P, carbon and C/N ratio in particle-size fractions of control, non-ingested soil and surface casts. Standard deviations are in parentheses.

Fractions (µm)	Mass (g·100 g^{-1})	Total P (µg·g^{-1} fraction)	Total P (µg·g^{-1} soil)	C (mg·g^{-1} fraction)	C (mg·g^{-1} soil)	C/N
Control						
Fl 200–2 000	2.26 (1.82)	1 604.7 (43.5)	36.3 (1.0)	205.1 (4.10)	4,64 (0.09)	20.72 (0.41)
F 20–2 000	85.56 (2.20)	80.7 (9.4)	69.0 (8.1)	15.4 (0.31)	13.18 (0.26)	14.00 (0.28)
F 2–20	9.19 (0.10)	448.9 (13.5)	41.3 (1.2)	42.0 (0.84)	3.86 (0.08)	12.35 (0.25)
F 0–2	4.18 (0.16)	958.2 (73.4)	40.1 (3.1)	45.1 (0.90)	1.89 (0.04)	8.20 (0.16)
	101.19 (0.15)		186.7 (3.4)		23.56 (0.47)	
Non-ingested soil						
Fl 200–2 000	1.17 (0.20)	1 734.8 (75.7)	20.3 (0.1)	346.1 (6.92)	4.05 (0.08)	26.22 (0.52)
F 20–2 000	79.86 (1.83)	50.1 (4.8)	40.0 (3.8)	12.2 (0.24)	9.74 (0.19)	15.25 (0.30)
F 2–20	12.03 (0.68)	542.8 (12.7)	65.3 (1.5)	48.5 (0.97)	5.83 (0.12)	12.12 (0.24)
F 0–2	6.92 (0.20)	872.7 (59.1)	60.4 (4.1)	45.6 (0.91)	3.16 (0.06)	9.30 (0.19)
	99.98 (1.87)		186.0 (6.9)		22.78 (0.46)	
Surface casts						
Fl 200–2 000	0.74 (0.20)	1 581.8 (20.9)	11.7 (0.2)	376.1 (7.52)	2.78 (0.05)	28.28 (0.57)
F 20–2 000	71.24 (0.96)	24.5 (5.3)	17.5 (3.8)	7.9 (0.16)	5.63 (0.11)	19.75 (0,39)
F 2–20	13.03 (0.60)	467,7 (18.0)	60.9 (2.4)	50.8 (1.02)	6.62 (0.13)	13.73 (0.27)
F 0-2	12.94 (0.91)	852.0 (19.3)	110.2 (2.5)	48.5 (0.97)	6.28 (0.13)	10.10 (0.20)
	97.95 (1.60)		200.3 (2.5)		21.31 (0.42)	

Table V. Inorganic, organic and total P concentrations and contents in $NaHCO_3$ and NaOH extracts of particle-size fractions. Values in parentheses represent the percentage of the P content in bulk sample.

Fractions (µm)	Inorganic P (µg P·g^{-1} fraction)	Inorganic P (µg P·g^{-1} soil)	Total P (µg P·g^{-1} fraction)	Total P (µg P·g^{-1} soil)	Organic P (µg P·g^{-1} soil)
$NaHCO_3$ 0.5 M					
Control					
F 20-2 000	5.19	4.44 a	4.38	3.75 a	0
F 2-20	4.58	0.42 a	24.12	2.22 a	1.80
F 0-2	10.88	0.45 a	63.6	2.66 a	2.20
		5.32 a (15.1)		**8.62** a (4.5)	**3.30** (2.1)
Ni					
F 20-2 000	2.20	1.76 b	7.65	6.11 b	4.36
F 2-20	4.70	0.57 b	32.07	3.86 b	3.29
F 0-2	12.34	0.85 b	55.66	3.85 b	3.00
		3.17 b (5.6)		**13.82** b (7.1)	**10.65** (7.8)
Casts					
F 20-2 000	1.60	1.14 c	5.09	3.63 a	2.49
F 2-20	11.61	1.51 c	18.18	2.37 a	0.86
F 0-2	18.46	2.39 c	47.44	6.14 c	3.75
		5.04 a (8.2)		**12.13** b (6.3)	**7.09** (5.4)
NaOH 0.1 N					
Control					
F 20-2 000	15.98	13.67 a	37.95	32.47 a	18.79
F 2-20	48.88	4.49 a	134.34	12.35 a	7.85
F 0-2	166.17	6.95 a	393.04	16.43 a	9.48
		25.11 a (79.7)		**61.24** a (32.1)	**36.13** (23.2)
Ni					
F 20-2 000	10.92	8.72 b	28.43	22.70 b	13.98
F 2-20	69.14	8.32 b	167.74	20.18 b	11.86
F 0-2	149.22	10.33 b	368.39	25.49 b	15.17
		27.36 a (48.2)		**68.37** a (35.3)	**41.01** (29.9)
Casts					
F 20-2 000	4.86	3.46 c	4.00	2.85 c	0
F 2-20	87.68	11.42 c	161.86	21.09 b	9.67
F 0-2	239.25	30.96 c	384.52	49.76 c	18.80
		45.85 b (74.8)		**73.70** a (38.2)	**27.85** (21.2)

In one extract and from a similar analysis, data in the same particle-size fraction with different letters significantly differ at $P < 5$ %.

(from 61.24 to 73.70 µg Pt·g^{-1} soil). Inorganic P content in NaOH extracts significantly increased from control and non-ingested soils to casts (*table V*). Organic P content was assessed as the difference between total and inorganic P values; therefore, extracted organic P content decreased from non-ingested soil to casts.

Control, non-ingested soil and surface casts showed markedly different distributions of P among the particle-size fractions. Inorganic and total P contents in the 20–2 000 µm fraction extracted by $NaHCO_3$ and NaOH decreased in both cases from control to non-ingested soil and casts (*table V*). Extracted total P content decreased from non-ingested soil to casts in $NaHCO_3$ extract and remained unchanged in the NaOH extract. As a result, the extracted inorganic P content significantly increased in both extracts from control to non-ingested soil and casts, with respective values of 0.42, 0.57 and 1.51 µg Pi·g^{-1} soil in $NaHCO_3$ extract and 4.49, 8.32 and 11.42 µg Pi·g^{-1} soil in NaOH extract. The same trend was observed in extracted inorganic and total P contents in the finest fraction (*table V*). Extraction produced in the 0–2 µm casts fraction 26.6 µg Pt·g^{-1} soil and 22.2 µg Pi·g^{-1} soil more than in the 0–2 µm non-ingested soil fraction.

4. DISCUSSION

These changes can be interpreted in terms of (i) a redistribution of P associated to clays, in relation with the fragmentation of unstable aggregates and a selective ingestion of fine particles and (ii) a mineralisation of organic phosphorus. The importance of earthworms affecting soil structure, organic matter processing and nutrient cycling has been recognised (for reviews, see [4, 18]).

4.1. Effect of *P. corethrurus* on soil texture and structure

In our study, the particle-size analysis of control and surface casts showed changes in the texture of materials with less coarse fractions and more fine ones in casts than in the control. This is probably due to a preferential ingestion of clay minerals as demonstrated by Barois et al. [2]. In laboratory conditions, *Pontoscolex corethrurus* produced fresh casts which are more dispersible than the control soil as indicated by a decrease in the proportion of large aggregates (from 18.9 to 7.7 %). Similar results had been obtained by Blanchart [5] with other species.

The particle-size fractions masses of the non-ingested soil (*table IV*) were intermediate between values measured in control and casts, and thus showed the dispersion and disaggregation effects of the remoistening of soil.

4.2. Effect of *P. corethrurus* on organic matter processes

Earthworms are also known to select the organic components that they ingest as demonstrated by Martin [21] with the earthworm *Millsonia anomala*. *Pontoscolex corethrurus* reduced the coarse organic matter fraction in fresh casts (0.74 g·100 g^{-1} soil), relative to control (2.26 g·100 g^{-1} soil) or non-ingested (1.17 g·100 g^{-1} soil) soils, as a result of comminution of ingested organic matter. The contents of carbon and nitrogen (*table II*) in earthworm casts were higher than in bulk soil due to the selective ingestion of organic particles. Many studies have indicated that earthworm casts are important microsites for some specific nutrient transformations (review in [4]). Earthworms produce a cutaneous mucus, an easily-assimilable organic matter, which might result in an activation of the soil microflora. Barois and Lavelle [1] found that *P. corethrurus* added large quantities of water and intestinal mucus to soil during transit through the gut, which resulted in a large increase in microbial activity in the gut and a smaller, although still detectable, increase in fresh casts as compared to the non-ingested soil. They suggested that the addition of readily-assimilable organic compounds during passage through an earthworm's gut resulted in an increased microbial degradation of complex organic substrates of the soil. Mineralisation occurred during the gut transit and possibly continued for a few hours after egestion of the casts. First the microbial flush due to remoistening and mixing of soil in the gizzard and then the mineralisation of organic matter were responsible for the decrease of the C/N ratio from control to non-ingested soil and from non-ingested soil to surface casts.

4.3. Effect of *P. corethrurus* on P dynamics

Tiwari et al. [31] reported higher microbial populations and enzyme activity, especially phosphatase, in field-collected casts than in bulk soil (sandy loam oxisol). Phosphorus availability in casts is often significantly greater than in bulk soils [15, 29, 31] as demonstrated for this ultisol by Chapuis and Brossard [8]. No change was observed in the total P contents between control, non-ingested soil and surface casts, but the decrease in organic P and the increase in inorganic P contents showed a greater mineralisation in casts than in bulk soil. Satchell and Martin [27] attributed the increased P availability in fresh casts to an increase in phosphatase activity in egested materials, although it remains unclear to what extent the increased phosphatase activity is due directly to earthworm-derived enzymes, or to increased microbial activity. In our study, the trend of changes in organic P did not allow to clarify this question but pointed out the activation of microbial activity by (i) moistening the soil and (ii) transit through an earthworm's gut.

Tropical soils often develop a high P-sorption capacity in relation to the nature of the clay minerals and López-Hernández et al. [19] suggested that gut passage also altered the P-sorption capacities of some tropical soils. The increase of phosphate in casts could be associated to the selective ingestion of fine soil particles [7]. The modifications of soil texture and structure led to a redistribution of phosphorus forms among the particle-size and chemical fractions, which resulted in a greater extractability of P in casts. The increased P content in the 0–2 μm fraction may be explained by the 6 % soil mass increase of this fraction due to the selective ingestion of fine particles. This value was obtained by calculating the difference between the masses of the 0–2 μm fraction in casts (12.94 %) and in non-ingested soil (6.92 %). Moistening of soil also produced disaggregation and a 2.7 % (6.92–4.18 %) increase of the 0–2 μm fraction mass. Particle selection operated by earthworms and aggregate instability induced an accumulation of P in the finest fraction.

5. CONCLUSION

Pontoscòlex corethrurus selectively ingest fine particles and produce fresh surface casts which are more dispersible than control and non-ingested soils. Phosphate is therefore more easily extractable in casts than in the non-ingested soil. Mineralisation of organic P may occur during the gut transit and possibly continues for a few hours after egestion of the casts. Digestion of fine plant residues probably has an impact on the P increase observed in the casts as compared to control and non-ingested soil. The approach used in this work has however some limitations, and only a massive ingestion of plant debris should lead to a significant effect on the chemical P balances. This study also points out the importance of using two control samples to distinguish remoistening and cutaneous mucus effects from digestion effects.

REFERENCES

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

[2] Barois I., Lavelle P., Brossard M., Tondoh J.E., Martinez M.A., Rossi J.P., Senapati B.K., Angeles A., Fragoso C., Jimenez J.J., Decaens T., Lattaud C., Kanyonyo ka Kajondo J., Blanchart E., Chapuis-Lardy L., Brown G., Moreno A., Ecology of species with large environmental tolerance and/or extended distributions, in: Lavelle P., Brussaard L., Hendrix P. (Eds.), The Potential for Management of Earthworm Activities in Tropical Agrosystems, CAB-I, Wallingford, 1999, pp. 38–60.

[3] Bartoli F., Burtin G., Herbillon A.J., Disaggregation and clay dispersion of oxisols. Na-resin, a recommended methodology for determining particle size distribution of oxisols rich in gibbsite, Trans. 15th Int. World Congr. ISSS (1990) 449–450.

[4] Blair J.M., Parmelee R.W., Lavelle P., Influences of earthworms on biogeochemistry, in: Hendrix P. (Ed), Earthworm Ecology and Biogeography in North America, CRC Press Inc., Boca Raton, 1995, pp. 127–158.

[5] Blanchart E., Rôle des vers de terre dans la formation et la conservation de la structure des sols de la savane de Lamto (Côte d'Ivoire), thèse de l'univ. Rennes-I, 1990.

[6] Bowman R.A., Cole C.V., Transformations of organic phosphorus substrates in soils evaluated by $NaHCO_3$ extraction, Soil Sci. 125 (1978) 49–54.

[7] Brossard M., Lavelle P., Laurent J.Y., Digestion of a vertisol by a endogeic earthworm (*Polypheretima elongata*, Megaloscolecidae) increases soil phosphate extractability, Eur. J. Soil Biol. 32 (1996) 107–111.

[8] Chapuis L., Brossard M., Modifications et stabilité du phosphore échangeable d'un ferralsol ingéré par un ver géophage, C. R. Acad. Sci. Paris IIa 320 (1995) 587–592.

[9] Duval L., Dosage céruléomolybdique de l'acide phosphorique dans les sols, les végétaux et les engrais, Ann. Agron. 13 (1962) 469–482.

[10] Feller C., Burtin G., Gérard B., Balesdent J., Utilisation des résines sodiques et des ultrasons dans le fractionnement granulométrique de la matière organique des sols. Intérêt et limites, Sci. Sol 29 (1991) 77–93.

[11] Hauser S., Distribution and activity of earthworms and contribution to nutrient recycling in alley cropping, Biol. Fertil. Soils 15 (1993) 16–20.

[12] James S.W., Soil, nitrogen, phosphorus, and organic matter processing by earthworms in tallgrass prairie, Ecology 72 (1991) 2101–2109.

[13] John M.K., Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid, Soil Sci. 109 (1970) 214–220.

[14] Kang B.T., Akinnifesi F.K., Pleysier J.L., Effect of agroforestry woody species on earthworm activity and physiochemical properties of worm casts, Biol. Fertil. Soils 18 (1994) 193–199.

[15] Krishnamoorthy R.V., Mineralization of phosphorus by faecal phosphatases of some earthworms of Indian tropics, Proc. Indian Acad. Sci. (Anim. Sci.) 99 (1990) 509–518.

[16] Laurent J.Y., Brossard M., Étude comparée de la détermination du phosphore total de sols tropicaux, Cah. Orstom sér. Pédol. 26 (1991) 281–285.

[17] Lavelle P., Barois I., Cruz I., Fragoso C., Hernandez A., Pineda A., Rangel A., Biological reasons for the success of the earthworm *Pontoscolex corethrurus* (Glossoscolecidae, Oligocheta) in the perturbated soil of the humid tropics, Biol. Fertil. Soils 5 (1987) 188–194.

[18] Lavelle P., Brussaard L., Hendrix P, The potential for management of earthworm activities in tropical agrosystems, CAB-I, Wallingford, 1999.

[19] López-Hernández D., Lavelle P., Fardeau J.C., Niño M., Phosphorus transformations in two P-sorption contrasting tropical soils during transit through *Pontoscolex corethrurus* (Glossoscolecidae: Oligochaeta), Soil Biol. Biochem. 25 (1993) 789–792.

[20] Mackay A.D., Springett J.A., Syers J.K., Gregg P.E.H., Origin of the effect of earthworms on the availability of phosphorus in a phosphate rock, Soil Biol. Biochem. 15 (1983) 63–73.

[21] Martin A., Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolicidae, Oligochaeta) of tropical savannas, on soil organic matter, Biol. Fertil. Soils 11 (1991) 234–238.

[22] McLaughlin J.R., Ryden J.C., Syers J.K., Development and evaluation of a kinetic model to describe phosphate sorption by hydrous ferric oxide gels, Geoderma 18 (1977) 295–307.

[23] Mulongoy K., Bedoret A., Properties of worm casts and surface soils under various plant covers in the humid tropics, Soil Boil. Biochem. 21 (1989) 197–203.

[24] Roche P., Grière L., Babre D., Calba H., Fallavier P., Le phosphore dans les sols intertropicaux : appréciation des niveaux de carence et des besoins en phosphore, Imphos-Gerdat, 1980.

[25] Rouiller J., Burtin G., Souchier B., La dispersion des sols dans l'analyse granulométrique. Méthode utilisant les résines échangeuses d'ions, Bull. ENSAIA Nancy 14 (1972) 193–205.

[26] Ryden J.C., McLaughlin J.R., Syers J.K., Mechanism of phosphate sorption of soils and hydrous ferric oxide gels, J. Soil Sci. 28 (1977) 72–92.

[27] Satchell J.E., Martin K., Phosphatase activity in earthworm faeces, Soil Biol. Biochem. 16 (1984) 191–194.

[28] Saunders W.M.H., Williams E.G., Observation on the determination of total organic phosphorus, J. Soil Sci. 6 (1955) 254–267.

[29] Sharpley A.N., Syers J.K., Potential role of earthworm casts for the phosphorus enrichment of runoff waters, Soil Biol. Biochem. 8 (1976) 341–346.

[30] Sharpley A.N., Syers J.K., Seasonal variation in casting activity and in the amounts and release to solution of phosphorus forms in earthworm casts, Soil Biol. Biochem. 9 (1977) 227–231.

[31] Tiwari S.C., Tiwari B.K., Mishra R.R., Microbial populations, enzyme activities and nitrogen-phosphorus-potassium enrichment in earthworm casts and in the surrounding soil of a pineapple plantation, Biol. Fertil. Soils 8 (1989) 178–182.