
ELSEVIER
Applied
Soil Ecology

Applied Soil Ecology 61 (2012) 161–168

Contents lists available at SciVerse ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Influence of earthworms and termites on runoff and erosion in a tropical steep slope fallow in Vietnam: A rainfall simulation experiment

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ARTICLE INFO

Article history:
Received 6 February 2012
Received in revised form 13 April 2012
Accepted 22 April 2012

Keywords:
Erosion
Earthworm
Termite
Biogenic aggregates
Rainfall simulation
Transfer

ABSTRACT

Earthworms and termites, as soil engineers, play a major role in the regulation of biogeochemical processes and the provision of ecosystem services. They create biogenic aggregates on the soil surface, e.g., earthworm casts and termite sheetings, which can influence soil erosion and the downward transfer of fertility. We assessed the effect of the micro-relief generated by earthworms and termites on soil hydrodynamic properties, and soil and nutrient losses. Eighteen 1 m × 1 m plots were established for rainfall simulation experiments (2 runs of 40 min rain, intensity 90 mm h^{-1}) in a steep slope fallow in Northern Vietnam. The soil surface of the micro-plots differed in the proportions of earthworm casts and termite sheetings. The results confirmed the importance of soil biostructures in the regulation of pedohydrological properties of soils. Although globular water-stable earthworm casts promote water infiltration in soil and decrease soil and nutrient losses, the unstable termite sheetings break-down rapidly and generate structural crusts which foster water runoff and soil detachment. No relation was observed between the abundance or biomass of earthworms or termites and the pedohydrological properties measured during the rainfall simulations. This therefore suggests that soil engineers can have greater impact on ecosystem functioning through their biogenic structures rather than as a result of their own abundance or biomass.

1. Introduction

Ecosystem engineers play a key role in modifying the chemical, physical and biological properties of their habitats (Jones et al., 1994, 1997). Earthworms, termites and ants are the major soil engineers (Lavelle et al., 1997; Jouquet et al., 2006) and their importance in the regulation of biogeochemical processes and ecosystem services, such as the supply of nutrients for plants and the maintenance of soil structure and water regulation, have been largely demonstrated (Lavelle et al., 2006). They produce or displace soil aggregates in and on top of the soil (i.e., biogenic aggregates), galleries and nest structures (the biopores), which impact soil physico-chemical properties, soil biodiversity and fertility (see Lavelle and Spain, 2005 for a review).

Soil erosion is a worldwide environmental and public health problem leading to direct losses of soil fertility and other on-site and off-site negative impacts such as reservoir siltation, water quality degradation and biodiversity loss (Pimentel, 2006). Land use change, with the loss of the protective vegetation cover, is frequently considered as the main human factor contributing to soil erosion (De Chazal and Rounsevell, 2009). For instance, there have been a considerable number of studies on the influence of vegetation cover on water infiltration, soil crust formation, and soil loss (Greene and Hairsine, 2004; Podwojewski et al., 2011 and references herein). However, several studies reported that soil engineers may also significantly influence water infiltration, soil erosion and the diffusion of nutrients throughout ecosystems. Although most of these studies were on earthworms (see Shipitalo and Le Bayon, 2004 for a review), several studies also demonstrated a significant impact of termites (Holt and Lepage, 2000; Jouquet et al., 2011b). Earthworm burrows, termite galleries and subterranean nest structures can increase water infiltration (Mando et al., 1996; Lamandé et al., 2003; Léonard et al., 2004; Blanco-Canqui and Lal, 2009) and then concomitantly reduce the risks of soil erosion. However, unstable biogenic aggregates (e.g., freshly emitted earthworm casts, termite sheetings) accumulated on the soil surface are prone to dislocation by the rain and can increase seal formation and soil erosion. Water stable aggregates (e.g., old earthworm casts and termite nests), on the other hand, enhance soil roughness, increase water infiltration, protect the soil

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0929-1393/$ – see front matter
http://dx.doi.org/10.1016/j.apsoil.2012.04.004

from crusting and thus decrease soil detachment (Nooren et al., 1995; Blanchart et al., 2004; Shipitalo and Le Bayon, 2004; Jouquet et al., 2004, 2008a, 2010). Surprisingly, very few studies have been conducted in sloping lands of the tropics which are characterized by intense rainfall events, soil degradation, rapid biogeochemical cycling and large populations of soil engineers. More information is therefore required on how soil engineers contribute to overland fluxes of matter and nutrients in tropical uplands.

The objective of this study was to assess the influence of earthworms and termites, as key soil bioturbators on soil hydrodynamics, as well as soil and nutrient losses. Rainfall simulations were conducted in a steep slope fallow in northeastern Vietnam on 1-m^2 micro-plots, which differed in the proportions of earthworm casts and termite sheetings. Our hypotheses were that (i) an increase in soil engineer abundance results in a concomitant enhancement of water infiltration and soil detachment rates and (ii) the soil microrelief created by earthworm and termite bioturbation significantly influences water runoff intensity, soil detachment rates and nutrient losses. We expected that highly stable earthworm casts would increase water infiltration and decrease soil detachment, whereas sheetings produced by termites are more prone to fragmentation and would thus increase soil detachment. As a consequence we assumed that earthworms favor the retention of nutrients and decrease the amount of dissolved nutrients lost with water runoff, whereas termites would increase nutrient leaching into runoff.

2. Material and methods

2.1. Description of the study site

This study was carried out in the experimental and long term monitoring catchment (46 ha) of the MSEC (Management Soil Erosion Consortium) project (Valentin et al., 2008). The study site is located in Dong Cao village, in north-eastern Vietnam, approximately 50 km south-west of Hanoi (20°57N, 105°29E). The annual rainfall ranges from 1500 to 1800 mm, of which 80–85% occurs from April to October. The air humidity is always high, between 75% and 100%. The mean daily temperature varies from 15 °C to 25 °C. The soil is an Acrisol (WRB, 1998).

The rainfall simulations were carried out in a 1 year fallow (3 ha) field where cattle grazing was temporarily excluded. In this ecosystem, the anecic earthworm *Amynthas khami* deposits globular water-stable casts (CAST) on the soil surface (Jouquet et al., 2008b). These biogenic structures can reach more than 20 cm in height but are often broken into smaller water stable aggregates by livestock trampling, human traffic and raindrop impacts (Fig. 1). Thus, most of CAST are dispersed on the soil surface without any links with subterranean galleries. The soil surface is also covered with smaller sized biogenic aggregates (<5 mm) but their origin is difficult to determine visually (Jouquet et al., 2009). They could come from the fragmentation of *A. khami*'s casts, the activity of other earthworm species (*Pheretima leucocirca*, *Ph. californica*, *Dichogaster modigliani* and other unidentified *Pheretima* sp., Mathieu et al., 2007) or the fragmentation of subangular aggregates produced through the action of plant roots or the mechanical disturbance of the soil surface (Jouquet et al., 2008a). Termites, especially fungus-growing termites (Macrotermitinae) and ants also produce free soil aggregates which are easily identifiable because of their small size (<1 mm) and granular shape, and because they are aggregated into sheetings which cover the litter (Fig. 1).

2.2. Rainfall simulations

Eighteen 1 m × 1 m plots were established for rainfall simulation experiments. The plots were bordered by iron frames inserted to a depth of 10 cm, as described by Janeau et al. (2003) and Ribolzi et al. (2011). The plots were selected so that they all had almost the same slope (∼37%, Table 1) but differed greatly in soil microrelief. The aerial biomass of the vegetation was carefully cut and plant residues were removed to avoid a protection of the soil surface by the vegetation cover.

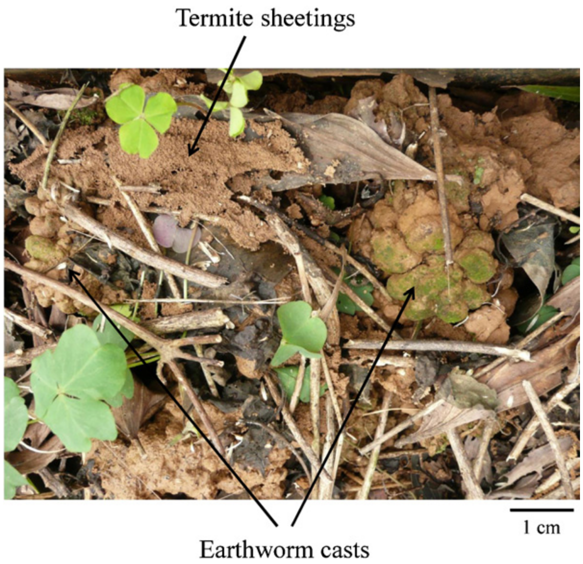

Fig. 1. Illustration of earthworm casts produced by *Amynthas khami* and termite sheetings covering the soil surface.
Photo: P. Jouquet (2011).

The plots were subjected to simulated rain with ORSTOM's portable field simulator (Casenave and Valentin, 1992) set 4 m above the floor, with a drop size distribution and kinetic energy similar to that of tropical rain of the same intensity (Asseline and Valentin, 1978). The multistage feet of the simulator's tower were adjusted to compensate for the slope differences and to simulate vertical rain. We calibrated the intensity by collecting the rain before each run and after simulation from an impermeable 1-m^2 pan placed directly over the plot. The experiments were conducted in March 2011, at the end of the winter season, to avoid natural rain disturbance. Two rainfall events (total amount of rain per event: TR = 60 mm) were simulated for 40 min in each plot (intensity 90 mm h^{-1}, ∼585 J m^{-2}) with approximately 24 h between the two runs. The two events corresponded to a return period of 10 years in the study watershed. The water used to simulate the rain was collected from a stream. This water had a pH of 6.6 and a low conductivity (∼95 μS).

For each plot and each run, the pre-runoff rainfall (Pr mm) was the volume of rainfall water necessary to cause runoff. Discharged water after runoff initiation was sampled every minute and was used to measure (i) the total volume of runoff water during the rainfall experiment (Lr mm), (ii) the volume of runoff water after the rainfall event (Dr mm), and (iii) the runoff water coefficient (KRx%), which is the ratio between the total amount of runoff water ($Lr + Dr$) and the total amount of rainfall water (TR).

Each water sample was filtered through GF/F membrane filters (Whatman, 0.7 μm porosity) to measure suspended solids and nutrient concentrations. Soil losses per run (SL_1 and SL_2 g m^{-2}) were obtained after drying at 60 °C and the cumulated amount of soil loss after the two runs ($SLt = SL_1 + SL_2$, g m^{-2}) was assessed using linear interpolation of fifteen 500 cm^3 samples per run. Water pH and conductivity were measured for each sample. Total nitrogen and phosphorus were evaluated in the filtrate solution according to Standard Methods for the Examination of Water and Wastewater (Clesceri et al., 1999). Total nitrogen was determined using

Table 1
Main physicochemical properties in the 0–10 cm soil layer before the rainfall experiment (SOIL, $n = 18$) and above-ground earthworm casts produced by *Amynthas khami* (CAST, $n = 9$): slope (%), bulk density ($g\,cm^{-3}$), moisture (% dry weight), particle size fraction (sand, silt and clay, in %), soil pH, CEC ($cmol\,kg^{-1}$), total C, N and P content (%). Standard errors are in parenthesis.

	Slope	Density	Moisture	Sand	Silt	Clay	pH_{KCl}	CEC	C	N	P
SOIL	36.9	0.98	49.3	28.9	31.0	39.5	3.8	14.7	2.25	0.19	0.17
	(1.0)	(0.12)	(1.1)	(1.2)	(0.6)	(0.9)	(0.0)	(0.8)	(0.11)	0.01	0.01
CAST				32.5	32.4	35.1	4.4	16.0	4.20	0.32	0.23
				(2.3)	(0.6)	(2.0)	(0.1)	(1.4)	(0.12)	0.01	0.02

the Kjeldahl method after digestion of the sample in sulfuric acid and total P was determined in water samples after sodium persulfate digestion and mineralization at 110 °C of the acidic phase. The exportation of N and P during the rainfall simulations were assessed by measuring the concentration of N and P in the rain water.

2.3. Soil analyses before the rainfall simulations

The soil bulk density (BD) of the upper 10 cm was assessed before the experiment in the direct vicinity of each plot with a 250 cm^3 cylinder. These cylinders were also used to assess soil moisture prior to the simulated rainfall events. Soil samples were also collected near the plots to assess the main soil physical and chemical properties. Soil texture was determined by the hydrometer method to obtain three particle size fractions: clay (<2 μm), silt (2–50 μm) and sand (50–2000 μm). Soil pH was determined after extraction in KCl (pH_{KCl}). Total soil C and N contents were determined according to the Walkley–Black and Kjeldahl methods, respectively. Total P content was determined with a spectrophotometer after acid digestion (H_2SO_4 and $HClO_4$). The cation exchange capacity (CEC) was determined using the ammonium acetate method at pH7.

Soil macrofauna abundance and diversity were assessed following the standard TSBF method (Anderson and Ingram, 1993). Soil sample blocks 25 cm × 25 cm wide × 30 cm deep were manually removed in the vicinity of the 1-m^2 plot and soil macroinvertebrates > 2 mm in size were removed by hand-sorting, counted, classified into taxonomic groups or at the morpho-species level and weighed (fresh weight) in the case of earthworms.

2.4. Evaluation of the soil micro-relief

Soil surface micro-relief was assessed according to the field method proposed by Casenave and Valentin (1992) before and after the two rainfall simulations. This method is frequently used in the tropics (i.e., Janeau et al., 2003; Podwojewski et al., 2008, 2011; Rouw et al., 2010) for the description of soil micro-relief. It consists in the visual determination of the proportions of surface occupied by gravel, litter residues, structural crust (CRUST), algae (ALGAE), free soil aggregates (i.e., aggregates on the soil surface and not anchored in the soil matrix) smaller (Ag < 2) or larger (Ag > 2) than 2 mm, earthworm globular casts produced by *A. khami* (CAST), and free aggregates deposited by termites (termite sheetings: TERMITE). Soil microrelief was assessed by two different scientists with a frame in wood dividing the surface of the plots into 100 squares (100 cm^2 each square). Their data were compared in order to reach precise description of the proportion of soil features. The proportion of gravel, plant residues and soil accumulated by ants was assessed in the field but not considered in this study because of the small areas that these features occupied. ALGAE included a community of organisms with different components such as microscopic algae, cyanobacteria, microfungi and mosses. Although it was impossible to determine the origin of Ag < 2 and Ag > 2, most of these soil aggregates were likely to come from the fragmentation of CAST or smaller earthworm casts produced by other earthworm species, or the accumulation on the soil surface of belowground soil aggregates associated with plant roots during weeding (Jouquet et al., 2009). In these soils, CRUST result from the tight packing of highly stable micro-aggregates (Janeau et al., 2003; Ribolzi et al., 2011).

2.5. Statistical analyses

Pearson correlation coefficients were used to express correlations among the main soil surface features. Relationships between earthworm abundance and biomass and the percentage of soil covered by free unidentified aggregates and CAST were tested through linear models. A two-way repeated measure analysis of variance (ANOVA), with time as the repeated measure, was used to assess the influence of the two rainfall simulation events on the soil features. Because the percentage of CAST, free aggregates and soil covered by algae did not vary during the experiment, these values were not integrated in the analysis. *T*-tests were used to assess differences in treatment means.

Linear regressions were used to assess the influence of the micro-relief made by earthworms and termites, and soil biodiversity (total number of soil macrofauna, total number of earthworm individuals, and total biomass of earthworms) on water infiltration, soil detachment and nutrient fluxes.

All statistical calculations were carried out using R (R Development Core Team, 2008). Differences among treatments were declared at the <0.05 probability level of significance.

3. Results

3.1. Initial soil properties, soil surface features and biodiversity

The slope, C, N and P contents, soil moisture, texture and bulk density of the surface horizon before the rainfall simulations were homogenous (Table 1). A wide range of CAST was recorded (from 0 to 70% of the soil surface). The surface percentage covered by free aggregates was also very high with surface ranging from 0.5 to 71% and from 3 to 73%, respectively for Ag < 2 and Ag > 2. Lower surface areas were recorded for CRUST (0.5–28%), TERMITE (0–18%), and ALGAE (0–4.5%).

Table 2
Correlation matrix between the main surface features (algae (ALGAE), structural crust (CRUST), free soil aggregates < 2 mm (Ag < 2), free soil aggregates > 2 mm (other than CAST) (Ag > 2), earthworm casts produced by *Amynthas khami* (CAST), and termite sheetings (TERMITE), in % soil surface).

	ALGAE	CRUST	Ag < 2	Ag > 2	CAST	TERMITE
ALGAE	1					
CRUST	−0.18	1				
Ag < 2	−0.19	0.35	1			
Ag > 2	0.20	0.11	0.57*	1		
CAST	0.62**	−0.48*	−0.34	−0.04	1	
TERMITE	−0.33	0.40	0.48*	0.33	−0.40	1

$n = 18$.
* $P < 0.05$.
** $P < 0.01$.

CAST were significantly and positively correlated with ALGAE and negatively correlated with CRUST (Table 2). In addition, Ag < 2 was positively correlated with Ag > 2 and with TERMITE.

In total, two termite morphospecies (one fungus-growing termite species and one soil feeding species) were sampled in only four plots. When present, the average density of termites was 420 ind m^{-2} (standard error, SE: 120). Earthworms were sampled in all the plots (average density: 171.6 ind m^{-2}, SE: 120; average weight: 44.4 g m^{-2}, SE: 32.9) and five earthworm morphospecies (*Ph. leucocirca* and four other morphospecies) were described. Except *Ph. leucocirca*, all individuals were juveniles and thus impossible to identify. *A. khami*, responsible for the edification of CAST, was not sampled. Interestingly, none of the surface features was linearly correlated to the abundance and biomass of the five earthworm species and the density of termites ($P > 0.05$ in all the cases).

3.2. Evolution of the soil surface after the two rainfall events

The soil micro-relief was slightly affected by the two rainfall events. In all the plots, the amount of CAST, ALGAE and free soil aggregates did not change. However, the soil surface covered by TERMITE and CRUST was affected by the two runs. While TERMITE initially covered 4.5% of the soil surface on average, the features disappeared after the first run. In contrast, the surface covered by CRUST increased from 3.4 (SE: 0.8) to 14.3% (SE: 3.1) in average ($P < 0.001$).

A significant negative linear regression was measured between the initial soil surface covered by CAST and CRUST measured after the two runs ($y = -0.29x + 19.01$, $R^2 = 0.36$, $P = 0.019$, Fig. 2). Conversely, positive linear regressions were measured between CRUST measured at the end of the experiment and the initial soil surface covered by CRUST ($y = 2.90x + 3.44$, $R^2 = 0.50$, $P = 0.003$) or TERMITE ($y = 0.89x + 9.48$, $R^2 = 0.54$, $P = 0.001$). All the other soil feature parameters, soil macrofauna abundance and earthworm biomass were not related to CRUST measured after the two runs ($P > 0.05$ in all the case).

3.3. Water runoff and soil loss

Correlations between soil features and hydrological properties and soil losses are shown in Table 3. For the first run, only CAST, CRUST, and TERMITE had an influence on water infiltration. Interestingly, CAST and CRUST had opposite effects. While CAST was negatively correlated with *Lr*, *Dr* and *KRx*, CRUST was positively correlated with the same variables. As a consequence, CAST led to a decrease in SL_1 while CRUST enhanced it. TERMITE was also positively related to *Dr* but it did not have an impact on other hydrological properties or soil losses. ALGAE, Ag < 2 and Ag > 2 did not correlate with any of the hydrological variables.

For the second run, the same trend was observed. CRUST had a positive effect on water runoff and soil loss (i.e., positive linear relation with *Lr*, *Dr*, *KRx* and SL_2) and we observed a negative relationship between CAST and the same variables. For all the significant linear regressions, R^2 values were higher after the second run than the first. TERMITE were not observed after the first run and it was therefore impossible to test their effects. No relationship was observed between the other soil surface features (ALGAE, Ag < 2 and Ag > 2) and the hydrological variables. Interestingly, no relationship was observed between *Pr* and the soil surface features for the two runs.

A significant negative linear regression was found between the initial soil surface covered by CAST and the total amount of soil lost (*SLt*) ($y = -0.90x + 62.10$, $R^2 = 0.40$, $P = 0.007$, Fig. 3). Conversely, the initial soil surface covered by CRUST was positively and linearly correlated to *SLt* ($y = 5.28x + 26.53$, $R^2 = 0.39$, $P = 0.012$). All the other soil feature parameters were not related to *SLt* ($P > 0.05$ in all the case). Soil macrofauna abundance and earthworm biomass were not related to any of the hydrological variables ($P > 0.05$ in all the case).

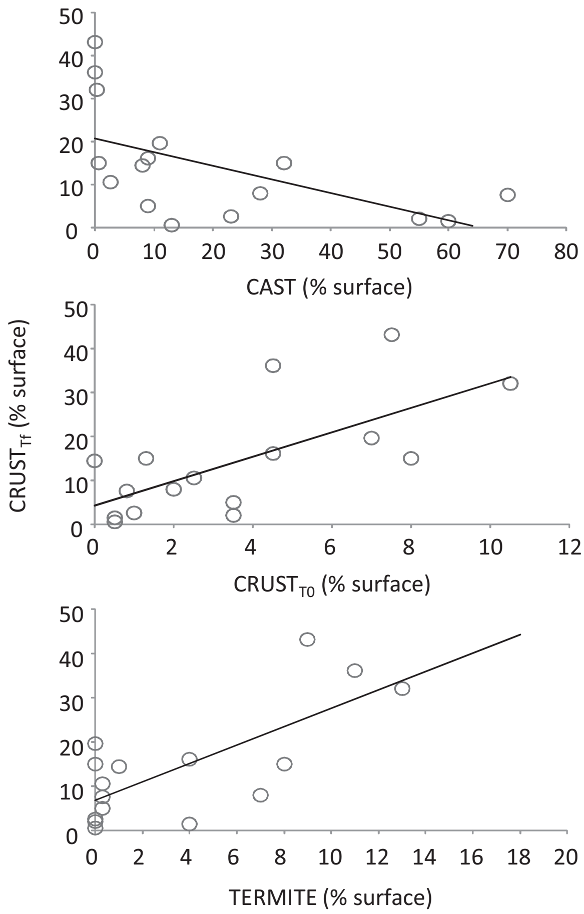

Fig. 2. Relationship between earthworm casts produced by *Amynthas khami* (CAST, %), the surface covered by structural crusts ($CRUST_{T0}$, %) or the soil sheetings made by termites (TERMITE, %) before the rainfall simulation and the surface covered by structural crusts at the end of the two simulated rainfall events ($CRUST_{Tf}$, %). Linear regression lines are fitted ($n = 18$).

3.4. Water runoff quality

Correlations between soil micro-relief and water runoff quality are shown in Table 4. CAST significantly decreased water conductivity (only for the first run) and increased water pH (for the two runs). Interestingly, although CAST enhanced the loss of dissolved P during the first run, negative linear regressions were found between CAST and the total amount of N and P in water runoff after the second run. Although CAST had different effects in the two runs, the overall effect of CAST on the loss of dissolved N and P remained negative ($y = -0.11x + 8.10$, $R^2 = 0.27$, $P = 0.032$, and $y = -0.11x + 7.99$, $R^2 = 0.44$, $P = 0.003$, respectively for N and P, Fig. 4a).

CRUST also had an important effect on water runoff quality. A negative linear regression was found between CRUST and water pH for both runs. Conversely, a positive linear regression occurred between CRUST and the total amount of N and P lost with water runoff. However, this regression was only significant for the second run. Finally, the overall effect of CRUST was to increase the quantity of N and P lost with water runoff ($y = 0.74x + 3.58$, $R^2 = 0.26$, $P = 0.039$, and $y = 0.60x + 3.88$, $R^2 = 0.29$, $P = 0.027$, respectively for N and P, Fig. 4b).

Table 3
Correlation between the main surface features (earthworm casts produced by *Amynthas khami* (CAST), structural crust (CRUST), termite sheetings (TERMITE), free soil aggregates < 2 mm (Ag < 2), free soil aggregates > 2 mm (other than CAST) (Ag > 2), and algae (ALGAE), in % soil surface) before the rainfall simulation (1st run) or after the first run (2nd run) and hydrological properties (*Pr*, *Lr*, *Dr*, *KRx*) and soil losses (*SL*) for the two runs of the rainfall simulation. Only significant results are displayed, ns = non significative regression, *n* = 18 samples.

		F	R^2	*P*-value
1st run				
CAST	Lr_1 (mm)	$-0.38x+30.95$	0.27	0.001
	Dr_1 (mm)	$-0.006x+0.43$	0.28	0.002
	KRx_1 (%)	$-0.64x+53.80$	0.28	0.001
	SL_1 (g m^{-2})	$-0.73x+55.2$	0.28	0.028
CRUST	Lr_1 (mm)	$2.73x+15.50$	0.28	0.029
	Dr_1 (mm)	$0.05x+0.15$	0.35	0.013
	KRx_1 (%)	$4.54x+25.80$	0.28	0.029
	SL_1 (g m^{-2})	$5.74x+21.21$	0.38	0.008
TERMITE	Dr_1 (mm)	$1.94x+85.46$	0.25	0.027
Ag < 2	ns			
Ag > 2	ns			
ALGAE	ns			
2nd run				
CAST	Lr_2 (mm)	$-0.49x+44.22$	0.39	0.007
	Dr_2 (mm)	$-0.008x+0.66$	0.35	0.012
	KRx_2 (%)	$-0.80x+73.39$	0.39	0.007
	SL_2 (g m^{-2})	$-0.90x+62.10$	0.45	0.003
CRUST	Lr_2 (mm)	$1.25x+20.44$	0.54	<0.001
	Dr_2 (mm)	$0.02x+0.26$	0.53	<0.001
	KRx_2 (%)	$2.06x+34.15$	0.53	<0.001
	SL_2 (g m^{-2})	$1.78x+24.29$	0.37	<0.001
Ag < 2	ns			
Ag > 2	ns			
ALGAE	ns			

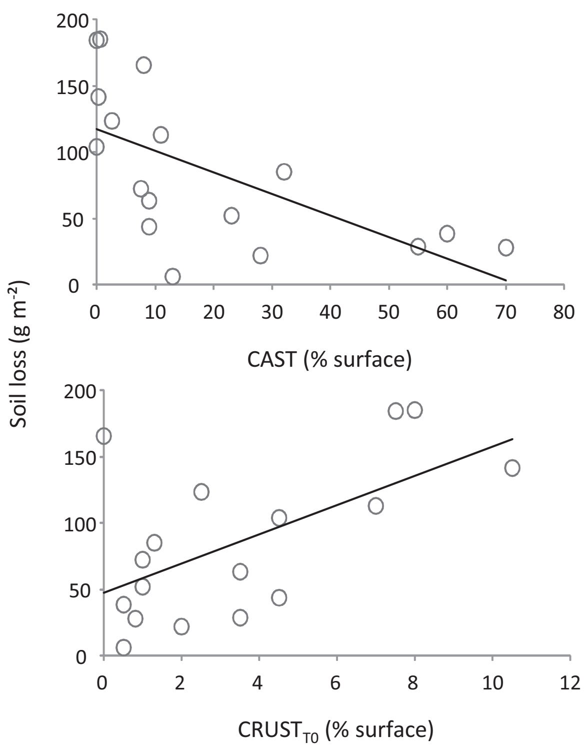

Fig. 3. Relationship between earthworm casts produced by *Amynthas khami* (CAST, %), the initial surface covered by structural crusts ($CRUST_{T0}$, %) and the quantity of soil loss measured after the two simulated rainfall events (soil loss, g m^{-2}). Linear regression lines are fitted (*n* = 18).

Table 4
Correlation between the main surface features (earthworm casts produced by *Amynthas khami* (CAST), structural crust (CRUST), termite sheetings (TERMITE), free soil aggregates < 2 mm (Ag < 2), free soil aggregates > 2 mm (other than CAST) (Ag > 2), and algae (ALGAE), in % soil surface) before the rainfall simulation (1st run) or after the first run (2nd run) and water runoff quality (conductivity, pH, and total amount of N and P) for the two runs of the rainfall simulation.

		F	R^2	*P*-value
1st run				
CAST	Conductivity (μS)	$-0.22x+92.00$	0.31	0.020
	pH_1	$0.008x+6.81$	0.33	0.016
	P_1 (mg m^{-2})	$1.94x+85.46$	0.25	0.011
CRUST	pH_1	$-0.06x+7.18$	0.38	0.009
TERMITE	pH_1	$-0.027x+7.09$	0.24	0.048
Ag < 2	ns			
Ag > 2	ns			
ALGAE	Ω_1 (μS)	$-3.67x+92.19$	0.27	0.032
2nd run				
CAST	pH_2	$0.008x+6.83$	0.31	0.019
	N_2 (mg m^{-2})	$-0.043x+3.94$	0.43	0.004
	P_2 (mg m^{-2})	$-0.005x+5.35$	0.49	0.001
CRUST	pH_2	$-0.02x+7.22$	0.45	0.003
	N_2 (mg m^{-2})	$0.11x+1.84$	0.60	<0.001
	P_2 (mg m^{-2})	$0.13x+1.80$	0.60	<0.001
Ag < 2	ns			
Ag > 2	Conductivity (μS)	$-0.14x+92.04$	0.24	0.046
ALGAE	P_2 (mg m^{-2})	$-0.67x+4.12$	0.24	0.046

Only significant results are displayed (*n* = 18 samples).

For the first run, TERMITE was negatively correlated with water pH and ALGAE correlated negatively to water conductivity. However, these two trends were not confirmed during the second run where TERMITE did not have an impact on the water quality and ALGAE did not affect water conductivity. A significant negative linear regression was measured between Ag > 2 and water conductivity for the second run. Finally, although ALGAE was significantly negatively correlated with total amount of *P* lost with runoff water for the second run, ALGAE did not affect the cumulated loss of P during the two runs (data not shown, *P* > 0.05).

No significant relationship was observed between the biodiversity variables and water runoff quality.

4. Discussion

4.1. Soil engineers influence soil surface features

Numerous studies have described the ability of soil engineers to modify soil micro-relief through the creation of biogenic structures or displacement of soil aggregates. However, how these biogenic aggregates interact with each other and the other main soil surface features remains unknown. At our field site, we previously observed that *A. khami* produces water-stable casts on the soil surface (CAST) (Jouquet et al., 2008a,b). Although it has a significant impact on soil surface characteristics, this earthworm species was not sampled in the top soil layer. Field observations reveal that this species is able to move rapidly down until deep soil layers when a perturbation occurs. This behavior explain why it was not sampled during our experiment, and thus the absence of a relationship between soil surface features (CAST, Ag < 2 and Ag > 2) and the diversity and abundance of earthworms in the first cm of the soil layer.

CAST was positively correlated with the surface occupied by ALGAE. Indeed, ALGAE were almost exclusively observed on CAST or small hills which probably corresponded to previous accumulations of CAST. Consequently, as suspected in a previous laboratory study (Jouquet et al., 2011a), CAST are likely to be long lasting structures in situ which can therefore act as refuges for the slow development of ALGAE. A positive feedback loop may even stabilize these CAST once they had been colonized by microphytes. Indeed,

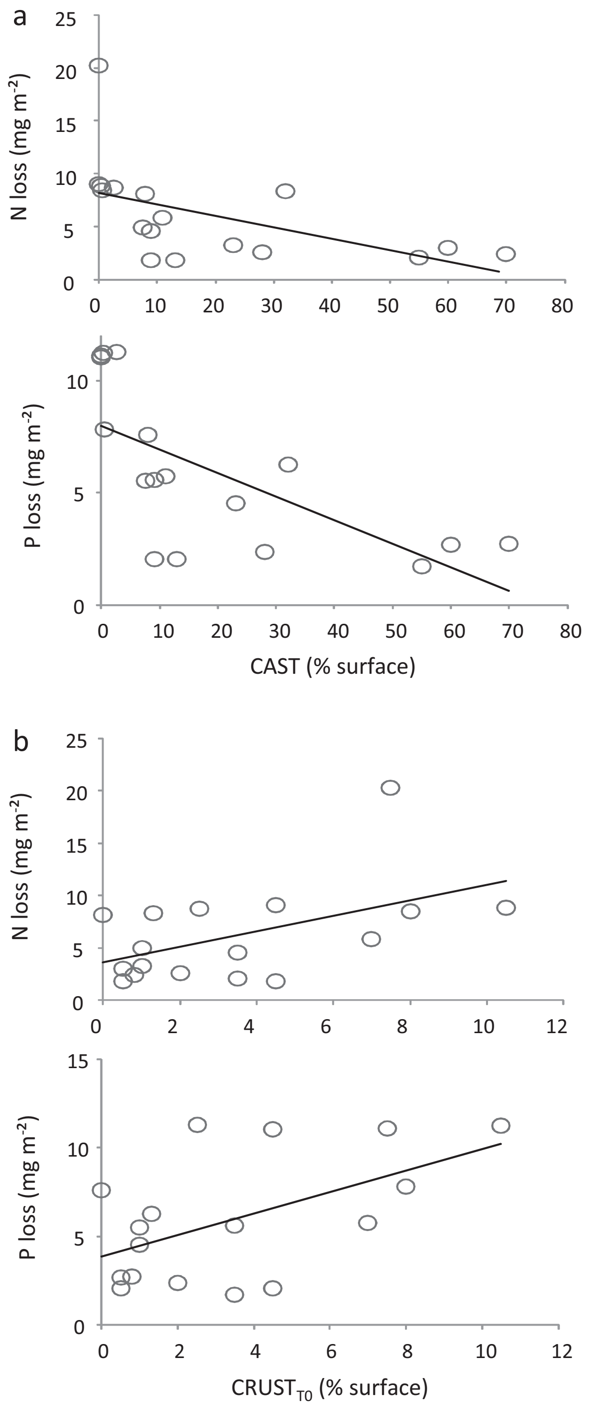

Fig. 4. Relationship between (a) earthworm casts produced by *Amynthas khami* (CAST, %) or (b) the initial surface covered by structural crusts ($CRUST_{T0}$, %) and the quantity of dissolved N and P measured in the water runoff after the two simulated rainfall events (mg m^{-2}). Linear regression lines are fitted ($n = 18$).

in drier areas ALGAE were reported to stabilize crusts (Malam Issa et al., 2009).

Interestingly, a negative relationship was observed between CAST and CRUST. CRUST are major structural features of surface soils. They are thin and highly dense soil layers which hamper water infiltration and foster soil detachment (Assouline, 2004). Their formation at the surface of bare soils exposed to the direct impact of raindrops is dominated by a wide variety of abiotic and biotic factors (Assouline, 2004; Fang et al., 2007). To date, researchers have seldom considered the influence of soil engineers on crust formation. However, our data suggest that the dynamics of CRUST is dependent on the initial presence of earthworm activities. How CAST negatively influence CRUST formation remains unknown but we assume that the high soil structural stability of CAST (Jouquet et al., 2008b) and their positive effect on water infiltration led to increased protection of the soil surface against crusting.

No correlation was observed between CAST and either type of free aggregate (Ag < 2 and Ag > 2), thus suggesting that CAST and these soil aggregates observed on the soil surface are not linked. These results are consistent with the specific organization of CAST observed by Jouquet et al. (2011a,b). Ag > 2 can be described as hierarchically organized aggregates with smaller aggregates (<500 μm) inside larger soil aggregates (500–2000 μm and 2000–5000 μm). CAST, however, appear to be a simple accumulation of small size aggregates < 500 μm. Consequently, the rain breaks CAST down into small size aggregates < 500 μm and this process is not linked with the formation of Ag < 2 and Ag > 2. Theoretically, the transport of these small size aggregates in water runoff could generate CRUST (Assouline, 2004) or increase soil loss. However, the negative relations between CAST and CRUST on one hand, and CAST and *SL* on the other hand suggest that the main impact of CAST was to improve the protection of the soil surface against crusting and soil loss.

The positive correlations of Ag < 2 with both Ag > 2 and TERMITE suggest that Ag < 2 can originate from: (1) termite foraging activity and the creation of sheetings made of small size aggregates cemented together with saliva (Holt and Lepage, 2000) and (2) the progressive fragmentation of bigger soil aggregates (Ag > 2) produced by earthworm species, other than *A. khami*, and/or plant roots.

4.2. Soil engineers influence water runoff and soil detachment

In this study, the key variables predicting water runoff and soil loss were highlighted by the gradual changes in soil surface features following the two simulated rainfall events. Free aggregates (Ag < 2 and Ag > 2) did not have an influence on water runoff and soil detachment. Despite the high rainfall intensity, these aggregates remained stable during the two runs. Surprisingly, in contrast to our first hypothesis, soil macrofauna abundance and diversity were not related to any of the variables describing water runoff and soil losses. However, as initially expected (hypothesis 2), although *A. khami* was never sampled, its casts have negative influences on water runoff and soil detachment. Indeed, CAST abundance lowered *Lr*, *Dr*, *KRx* and *SL*. These results therefore showed that: (i) the impact of soil engineers on ecosystem functioning can be through their biogenic structures (the casts of *A. khami* in our case) rather than necessarily due to their own abundance or biomass, and (ii) some soil engineer species, which can sometimes be less abundant or more difficult to observe (*A. khami* in this study), can play a much more important role in ecosystem functioning than other more abundant species (the five earthworm and two termite morphospecies found in our study site).

The mechanisms by which earthworm casts influence water runoff and soil loss were reviewed in Shipitalo and Le Bayon (2004) and Blanchart et al. (2004). In our case, CAST were not influenced by raindrop impacts because of their high water stability (Jouquet et al., 2008a,b). In a mechanism similar to stemflow (Levia and Frost, 2003; Muzylo et al., 2009; Lin, 2010), the interception of the raindrops by CAST also led to subsequently flow of rainwater down to the ground. This "castflow", together with increased soil roughness, slows water runoff velocity, and thus fosters water infiltration. Finally, although soil bulk density below CAST was not significantly different from that measured in areas without CAST (1.06 ± 0.10 and 0.98 ± 0.12 for soil bulk density below CAST and in areas without CAST, respectively), and because most of CAST were not anchored to the soil surface, it is likely that burrows below CAST also increased water infiltration (Bastardie et al., 2003; Lamandé et al., 2003; Zehe et al., 2010). This result is in agreement with Casenave and Valentin (1992) who showed that infiltration was clearly increased in semi-arid tropics where casts covered more than 20% of the soil surface. The net effect of earthworms on soil erosion remains unclear and is site specific (e.g., dependent on the earthworm species, soil properties and land slope) (Shipitalo and Protz, 1988; Le Bayon and Binet, 2001; Shipitalo and Le Bayon, 2004; Jouquet et al., 2010). In our study, the greater water infiltration in the presence of casts and their high stability, as shown by the non-fragmentation of CAST during the two runs, explained their negative effect on soil loss.

The second most important factor explaining the hydropedological variables measured in this study was the surface covered by CRUST. In our study, these soil surface features had exactly the opposite effect of CAST (i.e., in increasing *Lr*, *Dr*, *KRx* and consequently *SL*). These results are in agreement with several studies which reported the negative influence of crusts on soil permeability, water infiltration and soil detachment (Valentin, 1996; Assouline, 2004; Podwojewski et al., 2011). The negative impact of CAST on CRUST (shown in Table 2), showed that in addition to the above mention direct impacts of CAST on water infiltration and soil loss, CAST also indirectly improved water infiltration and decreased soil loss by decreasing the proportion of CRUST on the soil surface.

Termites produce galleries and below-ground nests which act as preferential channels that increase water infiltration (Holt and Lepage, 2000; Jouquet et al., 2011a,b). Consequently, the stimulation of termite activity generally leads to the perforation of crusts and an increase in water infiltration (Mando et al., 1996; Mando and Stroosnijder, 1999; Léonard et al., 2004). However, termite foraging activity can also lead to the creation of sheetings on the soil surface. Termite sheetings are made up of small aggregates slightly cemented together with saliva. Linear regressions demonstrated that CRUST were partly attributable to the fragmentation of these unstable biogenic aggregates on the soil. This finding confirmed observations made in the Côte d'Ivoire in Africa by Valentin et al. (2004). Due to the erosive effect of the first run, termite sheetings collapsed, leading to the creation and extension of existing crusts which enhanced water runoff and soil detachment. As a consequence, although statistically termite sheetings did not directly correlated with any of the hydropedological variables of this study, their foraging activity indirectly favored water runoff and soil detachment through the extension and formation of CRUST.

4.3. Soil engineers influence water runoff quality

The importance of soil engineers as major actors in nutrient cycling and hydrological processes has been widely acknowledged (see Lavelle and Spain, 2005 for a review). However, the retention or loss of dissolved forms of nutrients by earthworms and termites, with implications for nutrient management, has seldom been studied in steep-slope tropical ecosystems where the export of soluble nutrients in water runoff could drastically affect soil fertility and water quality.

Soil engineers have a strong influence on the availability of total and dissolved N and P in soil (Lavelle et al., 1992; Bignell and Eggleton, 2000; Mariani et al., 2007; Chapuis-Lardy et al., 2011; Jouquet et al., 2011a). In a laboratory experiment, Jouquet et al. (2007) found that the higher N content in CAST was associated with an increased diffusion of dissolved N in water. Although it is difficult to compare this result with those obtained in the present study made in situ without considering water infiltration, our findings suggest that CAST has a negative effect on the diffusion of nutrients in water runoff. Two hypotheses can be made: firstly, the high structural stability of CAST may have led to an increase in the retention of dissolved N and P, as well as ions in general, as shown by the negative effect of CAST on water conductivity and positive effect on water pH (i.e., lower flux of H^+). Another explanation lies in the fact that only water runoff was sampled during this experiment and a significant proportion of ions could have also leached out with infiltration water. Interestingly, CAST decreased the loss of dissolved N only during the second run and had a positive and then negative impact on P, during the first and second run, respectively. These latter results suggest that the dissolution of nutrients from CAST in water runoff was slowed down, progressive and not constant during the two rainfall simulation events. As a consequence, CAST not only favor water infiltration but also decrease soil and nutrient loss in water runoff.

Water runoff quality was also influenced by the development of CRUST on the soil surface. As expected from the hydropedological data, CRUST had exactly the opposite effect on the water runoff quality as CAST. The conductivity and quantity of dissolved N and P in water runoff increased and water runoff pH decreased when the proportion of CRUST increased.

5. Conclusion

The aim of this study was to determine how soil engineers affect the balance between processes that lead to the conservation or loss of matter and nutrients from the system. Our results suggest that soil engineers have a greater impact on ecosystem functioning through their soil biogenic structures (i.e., earthworm casts and termite sheetings) than due to their own abundance of biomass. A distinction between two types of biostructures can be inferred from our results. Although measurements made following rainfall simulations on 1-m^2 microplots cannot be generalized to describe overall hillslope dynamics, our results suggest that the globular and giant earthworm casts produced by *A. khami* tend to significantly improve water infiltration and decrease soil and nutrient losses in the field. On the other hand, granular termite sheetings were unstable, or less stable than the energy provided by the raindrop impacts. They collapsed and enhanced the surface of soil covered by CRUST and then indirectly enhanced water runoff and the export of soil and dissolved nutrients.

Acknowledgments

This project was supported financially by the French Institutes AFD (PAMPA/RIME project) and IRD through the unit research UMR 211 BIOEMCO and through the financial support of the JEAI-BioGEAQ. Loam and his colleagues are thanked for their help in the field. We acknowledge with gratitude Tran Minh Tien for his help in soil analyses and the SFRI (Soils and Fertilizers Research Institute) Vietnamese institute for providing access to the site.

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