Topsoil as affected by dung deposition under resting places of red howler monkey (*Alouatta seniculus*)

Sandrine Pouvelle, François Feer, Jean-François Ponge

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1 **Date of submission of the revised version:** January 29, 2008

2 **Name of authors:** Sandrine Pouvelle, François Feer, Jean-François Ponge

3 **Affiliation:** Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-

4 Château, 91800 Brunoy, France

5 **Corresponding author:** Jean-François Ponge, Tel.: +33 1 60479213, Fax: +33 1

6 60465009, E-mail: jean-francois.ponge@wanadoo.fr

7 **Potential reviewers:**

8 Dr Xingjun Tian, School of Life Science, Nanjing University, Nanjing 210093, People's

9 Republic of China, E-mail: tianxj@nju.edu.cn

10 Dr Karel Klinka, University of British Columbia, Forest Sciences Centre #3041, 2424

11 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada, Tel.: +1 604 822 3047, Fax:

12 +1 604 822 9102, E-mail: klinka@interchg.ubc.ca

13 Dr Takeda Hiroshi, Laboratory of Forest Ecology, Division of Environmental Science and

14 Technology, Graduate School of Agricultural Sciences, Kyoto University, 606-8502 Sakio-

15 Ku, Kyoto, Japan, Tel.: +81 757536080, Fax: +81 757536129, E-mail:

16 takedah@kais.kyoto-u.ac.jp

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Running Title: TOPSOIL EFFECTS OF DUNG DEPOSITION

Topsoil Effects of Dung Deposition under Red Howler Monkey (*Alouatta seniculus*) Resting Places

S. POUVELLE, F. FEER and J.F. PONGE

Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy (France). E-mail: ponge@mnhn.fr

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ABSTRACT

The short-term influence of dung deposition and its further redistribution by dung beetles was studied under a resting place of the red howler monkey (*Alouatta seniculus*) living in tropical rain forests of South America. Monkey dung was experimentally clumped on the field in a place used by troops of howler monkeys for resting (Nouragues reserve station, French Guiana). Dung-treated plots were sampled serially over three weeks and compared with controls located in their immediate vicinity. The composition of the soil matrix (top 10 cm) was studied in successive micro-layers by an optical method. Under the influence of dung beetle activity the topsoil became more homogeneous, losing its litter, its content in earthworm faeces increased in the course of time and surface mineral deposits

were penetrated by roots. The results were interpreted to the light of known effects of soil animal activity on plant growth and seedling survival.

Key Words: dung beetle activity, earthworm faeces, roots, tropical rain forests

INTRODUCTION

In the French Guianan primary rain forest, fruit-eating monkeys, in particular the most common red howler monkeys (*Alouatta seniculus* L.), defecate in places where troops (ca. 7 individuals each) are resting for night or some time of the day (Julliot, 1996a; Julliot *et al.*, 2001). Resting places are distributed over the whole territory of the troop and are used regularly or occasionally according to seasons (Julliot, 1992). Dung ($\sim 1.5 \text{ kg.day}^{-1}$ in each troop) is incorporated in a few hours in the topsoil through the burying activity of flying dung beetles which are olfactorily attracted to smears of fallen monkey faeces (Feer, 1999; Feer and Pincebourde, 2005). By this process the soil is locally enriched in fresh and nutrient-rich organic matter (Feeley, 2005), a sparsely distributed component of the tropical rain forest ecosystem (Cuevas and Medina, 1988; Burghouts *et al.*, 1998; Martius *et al.*, 2004), and in seeds of a variety of trees and lianas with pulp fruits (Julliot and Sabatier, 1993; Julliot, 1996b). As a result, a higher number of seeds and seedlings of forest plant species have been shown to occur under resting places of the howler monkey, thus pointing to the importance of this process for forest regeneration and richness in species (Julliot, 1997; Julliot *et al.*, 2001). The impact of this processing chain (Heard, 1994) on the composition of the topsoil is still unknown. Short- and long-term effects are expected, depending on the frequency with which resting sites are used by troops of howler monkeys.

The present study, undergone in French Guiana, was focused on the composition of the topsoil and the distribution of humus components (plant debris, roots, animal faeces) following dung deposition by howler monkeys. We selected a place which was used repetitively by the same troop of howler monkeys, a common pattern of their social behaviour (Julliot and Sabatier, 1993). This is a preliminary assessment of the effects of a processing chain involving plants (trees and lianas), vertebrates (monkeys) and invertebrates (dung beetles, soil animals) on soils of the tropical rain forest.

We used an optical method, which has been designed for the quantitative analysis of visually recognizable components of the topsoil in temperate (Bernier *et al.*, 1993; Peltier *et al.*, 2001) and tropical (Loranger *et al.*, 2003; Kounda-Kiki *et al.*, 2006) ecosystems.

MATERIALS AND METHODS

Study site and sampling procedure

The study site was a resting place used by a troop of howler monkeys, 100 m from the 'Nouragues' research station (French Guiana, 100 km south of the Atlantic Coast), which is located within a nature reservation from which human activities (hunting comprised) are excluded, and without any human settlement for several centuries (Charles-Dominique, 2001). The soil is a clayey Ferralsol, acid, yellowish, with a microaggregate texture of biological origin, and a sparsely distributed litter cover on the ground floor (Grimaldi and Riéra, 2001). The forest type is the equatorial rain forest, with canopy trees

as high as 50 m and a sparse understory (Poncy *et al.*, 2001). The annual rainfall averages 3000 mm, with a short dry season in September and October, and a mean annual temperature of 26.3°C (Grimaldi and Riéra, 2001).

The site was used by monkeys on 17 April 2004. Excrements were immediately collected then homogenized and grouped into clumps of near equal amount (~ 100g over 1 dm²) which were noted D1 to D4, their position being indicated in the field by a stamp, to be retrieved later once dung has disappeared from the ground surface. The soil was sampled at the same places at Day 12, 14, 21 and 23, respectively. Two control samples C1 and C2 were taken in the same site on Day 5 and 11, respectively, in places without any sign of recent defecation.

At the centre of each sampling plot, a block of surface soil 25 cm² in area and 10 cm depth was cut with a sharp knife, with as little disturbance as possible, and litter and soil underneath were carefully sampled. Each humus block was separated into individual layers that could be identified macroscopically on the base of structure, composition and other relevant properties (Kounda-Kiki *et al.*, 2006) or arbitrarily each cm when the soil was visually homogeneous. The various layers were transferred into polypropylene jars filled with 95% ethanol before transport to the laboratory. Care was taken that the jars were completely filled with the sampled material in order to avoid changes in structure resulting from shaking during transport to the laboratory.

Microscopical analyses

All 65 microlayers (~ 11 per soil block) were optically studied using the ‘small volume’ micromorphological method developed by Bernier and Ponge (1994), to which reference is made for details. Results from grid point counting (ca. 400 points) were expressed as the percentage of a given class of litter/humus component. A total of 158 classes of litter/humus components were identified (Appendix). The use of an eye reticle allowed to measure the size of organic or mineral particles or assemblages.

Plant debris were classified into leaves, cuticle/epidermis, petioles/nerves, stem/wood, bark, seeds, seed coats and according to the size of fragments. Roots and mycorrhizae were separated by colour and diameter in section. Animal faeces were classified by the size, the shape, the degree of mixing of mineral matter with organic matter and their state of transformation and assigned to animal groups using Bal (1982), Ponge (1991) and Topoliantz *et al.* (2000).

Data analyses

Percentages of occurrence of classes of litter/humus components in the 65 microlayers investigated were subjected to a correspondence analysis or CA (Greenacre, 1984). The different classes of litter/humus components were the active (main) variables, coded by their percentage of occurrence by volume. These components were classified into 61 gross categories, which were included as passive variables in the analysis.

All variables were transformed into $X=(x-m)/s+20$, where x is the original value, m is the mean of a given variable, and s is its standard deviation (Sadaka and Ponge, 2003). The addition to each standardized variable of a constant factor of 20 allows all values to be

positive, CA dealing only with positive numbers. Factorial coordinates of weighted variables (with constant mean and variance) can be interpreted directly in terms of their contribution to the factorial axes, contrary to raw data (Greenacre, 1984).

The volume percent of a given class (or gross category) of litter/humus components can be averaged over the whole profile (0-10 cm), taking into account the different micro-layers, each individual value being weighted by the thickness of the corresponding micro-layer. This allowed to calculate the mean percent volume of the different classes of litter/humus components and of the gross categories in each humus profile (Appendix).

RESULTS

When bulked over the 10 top cm, and when all components were pooled into 11 main gross categories, the composition of the six investigated humus profiles did not vary to a great extent (Fig. 1). In all six sample profiles, the topsoil was mainly made of earthworm mineral faeces, i.e. faeces with a poor content of organic matter given their light colour (Schulze *et al.*, 1993). However, the percentage of earthworm faeces in the top 10 cm (20 to 40%) increased steadily with time from the start of sampling (linear regression, $R^2 = 0.99$, $t = 14.1$, $P = 0.005$), beginning at a level lower than that of control samples. The second most abundant component was roots (20 to 30%), which did not increase with time but was higher in dung-treated samples than in controls (Mann-Whitney, $U = 4.7$, $P < 0.0001$). Earthworm hemorganic faeces were the second most abundant faecal component (7 to 15%) and earthworm holorganic faeces were nearly absent (<1%). Faeces of other animals (mainly enchytraeids, but also millipedes and termites, see Appendix) amounted to less than 10% of total solids. Non-root plant material

was but poorly represented (5 to 10%). Aggregates which could not be attributed to recent faecal deposition amounted to 10 to 30% of total solids. Over the six studied humus profiles, the distribution of mineral, hemorganic and holorganic categories was similar in aggregates and earthworm faeces ($\chi^2 = 0.61$, $P = 0.74$).

Differences between dung-treated and control samples were much more pronounced in the vertical distribution of topsoil components. The distribution of micro-layers and categories of humus components in the plane of the first two axes of CA (Fig. 2) showed that the composition of humus profiles varied according to depth, a complex of factors which was represented by Axis 1 (Fig. 3a). As expected, control samples exhibited a surface composition (see negative values of Axis 1) which contrasted greatly with that of deeper layers (positive values), but this contrast was much less pronounced in dung-treated samples. In control samples, the surface micro-layers were formed of plant material (roots and litter debris) and holorganic faeces (gross categories 32 to 57, all with negative values of Axis 1, with only a few exceptions) which were but badly represented at the surface of dung-treated samples.

Visual examples of the distribution of gross categories of topsoil components are given for root-permeated aggregates and faeces (Fig. 3b), earthworm mineral faeces (Fig. 3c) and root material (Fig. 3d). Root-permeated aggregates and faeces were present at the soil surface in dung-treated places then increased steadily with depth while in control samples they were absent in surface and present in a lesser amount underneath (Fig. 3b). Earthworm mineral faeces increased steadily from surface to deeper layers but they represented up to 30% of the soil matrix in the top 2 cm of dung-treated profiles while they were near absent at the same depth level in control samples. Root material (free roots, not

included onto faeces or aggregates) was more abundant at the soil surface and remained higher in content at depth in dung-treated samples than in control soil (Fig. 3d). An increase from 0 to 3-4 cm followed by a decrease was observed in the vertical distribution of root material in dung-treated samples, while this material decreased steadily in control samples.

DISCUSSION AND CONCLUSIONS

The topsoil under resting places of howler monkeys is mainly made of earthworm faeces of varying size and organic matter content, indicating a high level of biological activity through the stimulation of microbial processes and nutrient cycles (Lavelle *et al.*, 1998; Ponge, 2003). This can be compared with the higher level of plant recruitment which has been measured in these places (Julliot, 1997). Dung deposition (including seed of fleshy fruits) is followed by a chain of soil biological processes which embraces the burying action of dung beetles (Feer, 1999), the redistribution of organic and mineral matter by soil animals (Anderson, 1995) and the development of the root system of plants (Feeley, 2005).

When monkey dung is buried into the soil by dung beetles, deeper horizons (down to 40 cm) are excavated and pushed up to the surface, where they form small aerated mounds of yellow mineral soil resembling molehills (personal observations). We observed that these mounds, which are not protected by any litter cover, are rapidly flattened by canopy drip and disappear in a few days. Our study, done on the top 10 cm of soil, showed that the excavated soil, although poor in organic matter (light colour), became extensively colonized by earthworms and by roots within a few weeks (Fig. 1). Control samples did

not show any earthworm faecal material and any penetration of aggregates and faeces by roots in surface layers, while it was the case after dung application (Fig. 3b). The importance of earthworm faeces for the growth of the root system of plants has been observed and experimentally established (Tomati *et al.*, 1988), as well as their favourable role for soil structure (Blanchart, 1992) and water infiltration (Kladivko *et al.*, 1986). To the light of existing literature, it can be suspected that any event which favours earthworm activity will favour (i) the rapid development of the root system of trees and tree seedlings, the latter being of paramount importance for forest regeneration (Julliot *et al.*, 2001), (ii) the alleviation of ground floor toxicity following litter removal (Madge, 1965; Dalling and Hubbell, 2002). It should be noted, too, that seeds of a variety of tree species with fleshy fruits are concentrated in monkey dung (Julliot, 1996b) and that earthworms are known for the vertical redistribution of seed (Willems and Huijsmans, 1994) and their selective action on the soil seed bank (Thompson *et al.*, 1994; Decaëns *et al.*, 2003). All these aspects point to a rapid, positive feed-back involving monkeys, dung beetles and earthworms, favourable to the early and selective establishment of plant seedlings in a restricted array of favourable micro-sites (Harper *et al.*, 1965; Grubb, 1986; Dalling and Hubbell, 2002).

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7

Figure captions

Fig. 1. Composition in percent volume (gross categories) of the soil matrix in the top 10 cm of the six studied samples (D1 to D4 = dung-treated samples at Days 12, 14, 21 and 23; C1 and C2 = control samples)

Fig. 2. Projection of main categories (added as passive variables) and micro-layers of the six studied samples in the plane of the first two axes of CA (correspondence analysis). Codes of categories as in Appendix

Fig. 3. (a) Vertical distribution of Axis 1 values (CA)

(b) Vertical distribution of root-permeated faeces and aggregates

(c) Vertical distribution of earthworm mineral faeces

(d) Vertical distribution of roots

Fig. 1

Fig. 2

Fig. 3.

Appendix. List of categories identified in the soil matrix under the dissecting microscope, together with their mean percent volume and coordinates along Axis 1 of correspondence analysis

Code	Categories	D1	D2	D3	D4	C1	C2	Axis 1 (CA)
	Quartz particle 0-1 mm	1.08	0.50	0.49	0.74	2.79	0.87	-0.003
	Quartz particle 1-2 mm	0.61	0.50	0.42	0.05	0.14	0.19	0.011
	Quartz particle >2 mm	0.00	0.19	0.00	0.00	0.00	0.05	0.009
	Laterite particle	0.34	0.47	0.00	0.05	0.15	0.20	0.007
59	Enchytraeid faeces	2.73	2.69	7.51	4.20	2.15	2.16	0.017
	Earthworm mineral faeces <1 mm	3.95	4.13	3.56	4.60	6.95	5.33	0.018
	Earthworm mineral faeces 1-2 mm intact	2.11	1.94	1.87	2.05	2.74	2.94	0.017
	Earthworm mineral faeces 1-2 mm enchytraeid-tunnelled	2.36	5.05	5.01	4.36	2.18	1.54	0.022
	Earthworm mineral faeces 2-5 mm intact	0.86	0.62	1.50	1.13	1.70	2.58	0.015
	Earthworm mineral faeces 2-5 mm root-permeated	0.07	0.02	0.20	0.17	0.00	0.00	0.009
	Earthworm mineral faeces 2-5 mm enchytraeid-tunnelled	7.04	7.18	11.59	11.75	9.26	7.57	0.026
	Earthworm mineral faeces 2-5 mm root-permeated enchytraeid-tunnelled	1.59	1.59	1.42	2.17	0.43	0.19	0.018
	Earthworm mineral faeces 5-10 mm intact	0.00	0.07	0.17	0.00	0.23	0.45	0.006
	Earthworm mineral faeces 5-10 mm root-permeated	0.00	0.00	0.10	0.00	0.00	0.00	0.007
	Earthworm mineral faeces 5-10 mm enchytraeid-tunnelled	1.96	3.24	5.33	4.75	5.85	5.75	0.019
	Earthworm mineral faeces 5-10 mm root-permeated enchytraeid-tunnelled	1.67	2.16	3.51	3.50	1.04	0.63	0.019
	Earthworm mineral faeces 10-15 mm enchytraeid-tunnelled	0.10	0.00	0.43	0.87	0.18	1.36	0.011
	Earthworm mineral faeces 10-15 mm root-permeated enchytraeid-tunnelled	0.35	0.98	1.22	2.82	0.43	0.05	0.013
	Earthworm mineral faeces >15 mm intact	0.34	0.00	0.00	0.00	0.00	0.00	0.001
	Earthworm mineral faeces >15 mm enchytraeid-tunnelled	0.00	0.00	0.00	0.57	0.00	0.00	0.008
	Earthworm mineral faeces >15 mm root-permeated enchytraeid-tunnelled	0.00	0.00	0.55	2.51	0.00	0.00	0.010
	Mineral aggregate <1 mm	2.50	0.91	0.49	1.62	2.78	0.72	0.002
	Mineral aggregate 1-2 mm intact	0.22	0.00	0.00	0.17	0.88	0.14	-0.008
	Mineral aggregate 1-2 mm enchytraeid-tunnelled	1.67	1.06	1.14	0.75	0.47	0.29	0.012
	Mineral aggregate 2-5 mm intact	0.05	0.05	0.00	0.10	0.68	0.09	-0.011
	Mineral aggregate 2-5 mm root-permeated	0.00	0.00	0.00	0.00	0.10	0.00	0.002
	Mineral aggregate 2-5 mm enchytraeid-tunnelled	3.72	2.82	1.80	1.27	2.88	2.93	0.016
	Mineral aggregate 2-5 mm root-permeated enchytraeid-tunnelled	2.31	0.62	0.47	0.43	0.19	0.33	0.013
	Mineral aggregate 5-10 mm intact	0.05	0.00	0.00	0.00	0.22	0.00	-0.007
	Mineral aggregate 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
	Mineral aggregate 5-10 mm enchytraeid-tunnelled	2.98	1.84	1.11	0.63	3.91	4.02	0.015
	Mineral aggregate 5-10 mm root-permeated enchytraeid-tunnelled	4.82	1.56	1.10	1.32	0.67	0.53	0.014
	Mineral aggregate 10-15 mm intact	0.00	0.00	0.00	0.00	0.30	0.00	-0.012
	Mineral aggregate 10-15 mm root-permeated	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
	Mineral aggregate 10-15 mm enchytraeid-tunnelled	0.49	0.71	0.15	0.00	1.33	2.49	0.012
	Mineral aggregate 10-15 mm root-permeated enchytraeid-tunnelled	3.09	1.38	0.87	1.36	1.06	1.19	0.014
	Mineral aggregate >15 mm enchytraeid-tunnelled	0.49	0.00	0.00	0.20	0.38	0.67	0.012
	Mineral aggregate >15 mm root-permeated enchytraeid-tunnelled	2.09	0.97	1.11	1.69	0.29	0.00	0.012
	Earthworm hemorganic faeces <1 mm	0.85	0.45	0.31	0.26	0.68	1.31	-0.002
	Earthworm hemorganic faeces 1-2 mm intact	0.95	0.65	0.30	0.89	1.28	2.19	-0.002
	Earthworm hemorganic faeces 1-2 mm enchytraeid-tunnelled	0.68	0.84	0.35	0.43	0.24	0.92	0.005
	Earthworm hemorganic faeces 2-5 mm intact	0.73	0.43	0.57	0.38	0.63	1.76	0.000
	Earthworm hemorganic faeces 2-5 mm root-permeated	0.00	0.00	0.00	0.19	0.00	0.20	0.004
	Earthworm hemorganic faeces 2-5 mm enchytraeid-tunnelled	2.32	2.87	0.99	3.24	3.09	4.48	0.004
	Earthworm hemorganic faeces 2-5 mm root-permeated enchytraeid-tunnelled	0.29	0.29	0.05	1.05	0.14	0.10	0.007
	Earthworm hemorganic faeces 5-10 mm intact	0.05	0.00	0.20	0.14	0.09	0.10	0.007
	Earthworm hemorganic faeces 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.06	0.00	-0.011
	Earthworm hemorganic faeces 5-10 mm enchytraeid-tunnelled	0.89	0.83	0.59	3.28	1.67	2.08	0.006
	Earthworm hemorganic faeces 5-10 mm root-permeated enchytraeid-tunnelled	0.61	0.78	0.24	0.89	0.14	0.39	0.004
	Earthworm hemorganic faeces 10-15 mm intact	0.00	0.00	0.00	0.00	0.05	0.00	-0.013
	Earthworm hemorganic faeces 10-15 mm enchytraeid-tunnelled	0.00	0.10	0.00	0.59	0.19	0.24	0.003
	Earthworm hemorganic faeces 10-15 mm root-permeated enchytraeid-tunnelled	0.10	0.14	0.10	0.95	0.00	0.24	0.010
	Earthworm hemorganic faeces >15 mm root-permeated enchytraeid-tunnelled	0.00	0.12	0.19	0.00	0.00	0.00	0.002
	Hemorganic aggregate <1 mm	1.18	1.05	0.02	1.22	0.53	0.93	-0.005
	Hemorganic aggregate 1-2 mm intact	0.44	0.33	0.00	0.45	0.27	0.48	-0.015
	Hemorganic aggregate 1-2 mm enchytraeid-tunnelled	0.90	0.89	0.12	0.33	0.24	0.29	0.000
	Hemorganic aggregate 2-5 mm intact	0.05	0.14	0.00	0.21	0.27	0.20	-0.013
	Hemorganic aggregate 2-5 mm root-permeated	0.10	0.00	0.00	0.00	0.02	0.05	-0.008
	Hemorganic aggregate 2-5 mm enchytraeid-tunnelled	1.18	2.79	0.17	0.95	0.39	1.84	0.000
	Hemorganic aggregate 2-5 mm root-permeated enchytraeid-tunnelled	0.22	1.03	0.00	0.40	0.00	0.20	0.000
	Hemorganic aggregate 5-10 mm intact	0.00	0.00	0.00	0.00	0.20	0.00	-0.013
	Hemorganic aggregate 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.12	0.00	-0.013
	Hemorganic aggregate 5-10 mm enchytraeid-tunnelled	0.15	1.35	0.29	0.87	0.49	1.40	0.004
	Hemorganic aggregate 5-10 mm root-permeated enchytraeid-tunnelled	0.46	1.02	0.31	0.52	0.15	0.63	0.004
	Hemorganic aggregate 10-15 mm enchytraeid-tunnelled	0.25	0.12	0.42	0.14	0.00	0.71	0.007
	Hemorganic aggregate 10-15 mm root-permeated enchytraeid-tunnelled	0.20	0.58	0.33	0.80	0.29	0.54	0.004
	Hemorganic aggregate >15 mm root-permeated	0.00	0.00	0.00	0.00	0.00	0.54	0.004
	Hemorganic aggregate >15 mm enchytraeid-tunnelled	0.00	0.14	0.00	0.00	0.00	0.00	0.004
	Hemorganic aggregate >15 mm root-permeated enchytraeid-tunnelled	0.00	0.33	0.00	0.00	0.00	0.10	0.001
	Earthworm hologanic faeces <1 mm	0.00	0.00	0.00	0.00	0.05	0.05	0.001
	Earthworm hologanic faeces 1-2 mm	0.00	0.00	0.00	0.00	0.05	0.00	0.003
	Earthworm hologanic faeces 2-5 mm	0.00	0.00	0.00	0.00	0.24	0.09	-0.001
	Earthworm hologanic faeces 5-10 mm	0.05	0.00	0.00	0.00	0.10	0.05	-0.004
	Hologanic aggregate <1 mm	0.00	0.00	0.00	0.02	0.22	0.05	-0.006
	Hologanic aggregate 1-2 mm	0.10	0.00	0.00	0.00	0.17	0.00	-0.005
	Hologanic aggregate 2-5 mm	0.10	0.05	0.00	0.00	0.40	0.15	-0.016
	Hologanic aggregate 5-10 mm	0.05	0.00	0.00	0.00	0.29	0.20	-0.008
	Hologanic aggregate 10-15 mm	0.00	0.00	0.00	0.00	0.06	0.10	0.000
60	Millipede faeces	0.09	0.00	0.40	0.00	0.00	0.00	0.009
61	Termite faeces	0.00	0.00	0.00	0.00	0.00	0.77	0.009
	Leaf fragment <2 mm	0.05	0.10	0.14	0.35	0.06	0.13	-0.006
	Leaf fragment 2-5 mm	0.94	0.39	0.48	0.76	0.87	0.60	-0.015
	Leaf fragment 5-10 mm	0.89	0.34	0.47	0.49	1.48	0.82	-0.016

	Leaf fragment >10 mm	0.50	1.77	1.11	0.49	0.83	1.04	-0.005
	Cuticle/epidermis fragment <2 mm	0.05	0.21	0.02	0.07	0.02	0.04	-0.007
	Cuticle/epidermis fragment 2-5 mm	0.00	0.14	0.02	0.05	0.19	0.00	-0.008
	Cuticle/epidermis fragment 5-10 mm	0.00	0.00	0.00	0.00	0.13	0.00	-0.011
	Petiole/nerve fragment <2 mm	0.05	0.02	0.00	0.00	0.31	0.00	-0.020
	Petiole/nerve fragment 2-5 mm	0.35	0.02	0.00	0.02	0.24	0.00	-0.004
	Petiole/nerve fragment 5-10 mm	0.10	0.05	0.00	0.00	0.13	0.04	-0.010
	Petiole/nerve fragment >10 mm	0.05	0.00	0.00	0.12	0.00	0.18	-0.008
	Stem/wood fragment <2 mm	0.00	0.02	0.26	0.00	0.53	0.51	-0.018
	Stem/wood fragment 2-5 mm	0.29	0.02	0.07	0.00	1.05	0.22	-0.021
	Stem/wood fragment 5-10 mm	0.05	0.00	0.15	0.00	0.00	0.04	0.001
	Stem/wood fragment >10 mm	0.00	0.15	0.00	0.28	0.06	0.10	-0.002
	Bark fragment <2 mm	0.98	1.00	1.32	0.94	1.55	0.48	0.002
	Bark fragment 2-5 mm	0.66	0.70	0.94	0.55	1.56	1.52	-0.016
	Bark fragment 5-10 mm	0.05	0.19	0.38	0.26	0.58	0.88	-0.014
	Bark fragment >10 mm	0.05	0.00	0.05	0.02	0.00	1.12	-0.008
	Seed coat fragment <2 mm	0.00	0.00	0.00	0.00	0.06	0.00	-0.011
	Seed coat fragment 2-5 mm	0.00	0.12	0.26	0.00	0.06	0.00	0.001
	Seed coat fragment 5-10 mm	0.05	0.00	0.35	0.09	0.00	0.00	0.006
	Seed coat fragment >10 mm	0.00	0.05	1.14	0.24	0.50	0.18	-0.001
	Seed <2 mm	0.00	0.02	0.02	0.00	0.00	0.00	0.001
	Seed 2-5 mm	0.10	0.00	0.00	0.00	0.00	0.00	0.002
	Seed 5-10 mm	0.00	0.02	0.14	0.05	0.00	0.00	0.006
	Seed >10 mm	1.59	0.71	0.70	0.00	0.00	0.00	0.001
	Club moss (Selaginella)	0.00	0.00	0.00	0.02	0.13	0.04	-0.014
	Mycelium	0.05	0.00	0.07	0.00	0.05	0.05	0.003
	Black rhizomorph	0.07	0.02	0.02	0.05	0.17	0.05	-0.004
	White rhizomorph	0.05	0.02	0.00	0.00	0.20	0.09	-0.019
	Miscellaneous (humified or unidentified) plant material	2.07	0.80	0.26	0.72	0.55	0.99	-0.007
	Charcoal	0.05	0.10	0.23	0.09	0.00	0.00	0.004
	Fruit fragment	0.02	0.05	0.19	0.00	0.24	0.00	0.011
	Bud	0.00	0.00	0.00	0.00	0.05	0.00	-0.001
	Black root Ø <0.5 mm	0.05	0.07	0.23	0.00	0.05	0.09	0.005
	Black root Ø 0.5-1 mm	0.15	0.19	0.57	0.07	0.20	0.76	0.004
	Black root Ø 1-2 mm	0.05	0.17	0.57	0.00	0.00	0.86	0.006
	Brown root Ø <0.5 mm	4.28	6.92	6.91	7.60	5.19	0.77	0.002
	Brown root Ø 0.5-1 mm	7.22	6.97	4.93	8.10	3.02	2.35	0.002
	Brown root Ø 1-2 mm	2.54	3.99	6.06	4.90	1.57	0.88	0.007
	Brown root Ø >2 mm	1.31	3.59	10.37	3.02	0.29	0.63	0.010
	Beaded root Ø <0.5 mm	0.02	0.16	0.00	0.00	0.57	0.00	-0.006
	Beaded root Ø 0.5-1 mm	1.15	2.96	0.23	0.86	2.39	2.63	-0.016
	Beaded root Ø 1-2 mm	1.07	1.46	0.14	0.45	0.72	3.09	-0.010
	Beaded root Ø >2 mm	0.10	0.00	0.00	0.00	0.20	1.90	-0.005
	Detached bead (from beaded root)	0.49	0.84	0.23	0.22	0.27	0.78	-0.002
	Red root Ø <0.5 mm	0.02	0.05	0.00	0.00	0.25	0.05	-0.010
	Red root Ø 0.5-1 mm	0.00	0.33	0.19	0.00	0.10	0.73	-0.006
	Red root Ø 1-2 mm	0.00	0.19	0.00	0.00	0.05	0.27	-0.007
	Light-brown root Ø <0.5 mm	3.06	1.35	0.05	0.96	0.33	1.50	0.011
	Light-brown root Ø 0.5-1 mm	1.40	0.87	0.05	1.46	1.19	1.99	0.004
	Light-brown root Ø 1-2 mm	0.50	0.05	0.00	0.10	0.33	0.58	0.009
	Light-brown root Ø >2 mm	0.00	0.00	0.00	0.00	0.29	0.00	0.005
	White root Ø <0.5 mm	0.86	0.17	0.24	0.89	0.66	0.39	0.000
	White root Ø 0.5-1 mm	0.00	0.05	0.14	0.40	0.00	0.10	0.010
	White root Ø 1-2 mm	0.05	0.00	0.00	0.00	0.00	0.00	0.007
	White root with hairs Ø <0.5 mm	0.05	0.07	0.00	0.00	0.11	0.24	-0.002
	White root with hairs Ø 0.5-1 mm	0.00	0.00	0.00	0.00	0.00	0.36	-0.009
	White root with hairs Ø 1-2 mm	0.00	0.00	0.00	0.00	0.00	0.09	-0.009
	White root with hairs Ø >2 mm	0.00	0.00	0.00	0.00	0.00	0.04	-0.009
	Root with claret-coloured mycorrhizae Ø <0.5 mm	0.00	0.10	0.00	0.00	0.51	0.00	-0.011
	Root with claret-coloured mycorrhizae Ø 0.5-1 mm	0.15	0.14	0.00	0.00	1.81	0.00	-0.016
	Root with claret-coloured mycorrhizae Ø 1-2 mm	0.05	0.00	0.00	0.00	0.13	0.00	-0.011
	Root with claret-coloured mycorrhizae Ø >2 mm	0.00	0.00	0.00	0.00	0.20	0.00	-0.010
	Root with orange mycorrhizae Ø <0.5 mm	0.00	0.00	0.00	0.09	0.00	0.00	0.010
	Root with orange mycorrhizae Ø 0.5-1 mm	0.00	0.00	0.00	0.34	0.22	0.00	-0.010
	Root with orange mycorrhizae Ø 1-2 mm	0.00	0.00	0.00	0.14	0.00	0.00	0.010
	Root fragment	0.42	0.45	0.26	0.05	0.91	0.14	-0.006
	Voided root Ø <0.5 mm	0.10	0.14	0.05	0.02	0.27	0.09	-0.011
	Voided root Ø 0.5-1 mm	0.59	0.57	0.10	0.00	0.89	0.49	-0.013
	Voided root Ø 1-2 mm	0.07	0.00	0.19	0.02	0.15	0.15	0.005
	Root fibers	0.27	0.33	0.47	0.41	0.19	0.05	0.009
	Ant	0.00	0.00	0.00	0.05	0.00	0.00	0.007
	Potworm (Enchytraeida)	0.00	0.00	0.09	0.14	0.00	0.00	0.004
	Insect larva	0.00	0.00	0.00	0.00	0.00	0.04	-0.009
	Arthropod cuticle	0.24	0.10	0.07	0.00	0.10	0.18	0.000
	Arthropod	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
1	Total quartz particles	1.69	1.20	0.91	0.79	2.93	1.11	0.000
2	Total mineral particles	2.04	1.67	0.91	0.84	3.08	1.31	0.002
3	Total earthworm mineral faeces 1-2 mm	4.47	6.98	6.88	6.41	4.92	4.48	0.025
4	Total earthworm mineral faeces 2-5 mm	9.56	9.41	14.71	15.20	11.39	10.35	0.027
5	Total earthworm mineral faeces 5-10 mm	3.63	5.47	9.11	8.25	7.12	6.82	0.021
6	Total earthworm mineral faeces 10-15 mm	0.44	0.98	1.66	3.69	0.61	1.41	0.014
7	Total earthworm mineral faeces >15 mm	0.34	0.00	0.55	3.07	0.00	0.00	0.009
8	Total earthworm mineral faeces	22.40	26.98	36.47	41.23	30.99	28.38	0.027
9	Total mineral aggregates 1-2 mm	1.89	1.06	1.14	0.92	1.35	0.43	0.007
10	Total mineral aggregates 2-5 mm	6.08	3.49	2.26	1.79	3.84	3.35	0.015
11	Total mineral aggregates 5-10 mm	7.85	3.40	2.20	1.95	4.82	4.55	0.016
12	Total mineral aggregates 10-15 mm	3.58	2.09	1.02	1.36	2.71	3.68	0.014
13	Total mineral aggregates >15 mm	2.59	0.97	1.11	1.89	0.66	0.67	0.014
14	Total mineral aggregates	24.49	11.93	8.22	9.53	16.16	13.40	0.016
15	Total mineral aggregates with roots	15.99	9.29	10.54	15.96	4.25	2.93	0.021
16	Total mineral material	51.65	43.27	53.11	55.80	52.39	45.26	0.028
17	Total earthworm hemorganic faeces 1-2 mm	1.64	1.49	0.66	1.32	1.52	3.11	0.000

18	Total earthworm hemorganic faeces 2-5 mm	3.34	3.60	1.61	4.86	3.87	6.53	0.003
19	Total earthworm hemorganic faeces 5-10 mm	1.55	1.62	1.02	4.31	1.97	2.57	0.005
20	Total earthworm hemorganic faeces 10-15 mm	0.10	0.24	0.10	1.55	0.24	0.48	0.006
21	Total earthworm hemorganic faeces >15 mm	0.00	0.12	0.19	0.00	0.00	0.00	0.002
22	Total earthworm hemorganic faeces	7.47	7.52	3.88	12.30	8.28	14.00	0.002
23	Total hemorganic aggregates 1-2 mm	1.34	1.22	0.12	0.78	0.51	0.77	-0.010
24	Total hemorganic aggregates 2-5 mm	1.54	3.96	0.17	1.56	0.68	2.28	-0.005
25	Total hemorganic aggregates 5-10 mm	0.61	2.38	0.60	1.39	0.96	2.02	-0.004
26	Total hemorganic aggregates 10-15 mm	0.45	0.70	0.75	0.95	0.29	1.25	0.005
27	Total hemorganic aggregates >15 mm	0.00	0.48	0.00	0.00	0.00	0.64	0.002
28	Total hemorganic aggregates	5.12	9.78	1.66	5.90	2.98	7.90	-0.006
29	Total hemorganic aggregates with roots	1.98	4.30	1.22	4.81	0.94	2.98	0.001
30	Total aggregates with roots	17.97	13.59	11.76	20.77	5.19	5.91	0.020
31	Total hemorganic material	12.59	17.30	5.54	18.20	11.26	21.90	-0.003
32	Total earthworm holorganic faeces	0.05	0.00	0.00	0.00	0.43	0.19	-0.004
33	Total holorganic aggregates	0.24	0.05	0.00	0.02	1.13	0.49	-0.015
34	Total leaf fragments	2.38	2.61	2.20	2.09	3.25	2.60	-0.011
35	Total cuticle/epidermis fragments	0.05	0.36	0.05	0.12	0.34	0.04	-0.012
36	Total petiole/nerve fragments	0.55	0.10	0.00	0.14	0.67	0.22	-0.015
37	Total stem/wood fragments	0.34	0.20	0.48	0.28	1.64	0.88	-0.024
38	Total bark fragments	1.73	1.90	2.68	1.78	3.70	4.00	-0.015
39	Total seed coat fragments	0.05	0.17	1.75	0.33	0.63	0.18	-0.001
40	Total seeds	1.69	0.76	0.86	0.05	0.00	0.00	0.001
41	Total non-root plant material	6.79	6.09	8.03	4.79	10.22	7.92	-0.015
42	Total black roots	0.25	0.43	1.37	0.07	0.24	1.71	0.005
43	Total brown roots	15.36	21.48	28.27	23.61	10.07	4.62	0.006
44	Total beaded roots	2.84	5.43	0.60	1.53	4.16	8.41	-0.015
45	Total red roots	0.02	0.57	0.19	0.00	0.39	1.05	-0.010
46	Total light-brown roots	4.95	2.27	0.10	2.52	2.14	4.08	0.009
47	Total white roots	0.91	0.21	0.38	1.30	0.66	0.49	0.003
48	Total white roots with hairs	0.05	0.07	0.00	0.00	0.11	0.74	-0.010
49	Total roots with claret-coloured mycorrhizae	0.20	0.24	0.00	0.00	2.64	0.00	-0.019
50	Total roots with orange mycorrhizae	0.00	0.00	0.00	0.57	0.22	0.00	-0.008
51	Total roots	25.00	31.15	31.18	29.65	21.56	21.23	-0.007
52	Total roots Ø <0.5 mm	8.35	8.89	7.44	9.54	7.68	3.04	0.000
53	Total roots Ø 0.5-1 mm	10.07	11.52	6.11	11.23	8.93	8.93	-0.012
54	Total roots Ø 1-2 mm	4.26	5.85	6.76	5.59	2.80	5.77	-0.003
55	Total roots Ø >2 mm	1.41	3.59	10.37	3.02	0.97	2.57	0.007
56	Total voided roots	0.76	0.71	0.33	0.05	1.30	0.73	-0.013
57	Total plant material	34.90	39.14	40.46	35.65	34.24	30.96	-0.020
58	Total animal material	0.24	0.10	0.16	0.19	0.12	0.23	-0.005