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Andosol-forming process linked with soil fauna under the perennial grass *Mulhembergia macroura*

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Abstract

On the Cofre de Perote volcano, Mexico, at an elevation of 3000 m, vegetation is dominated by pine trees and *Mulhembergia macroura* grass. The grass undergoes a specific decomposition process whereby dead leaves and roots at different stages of decomposition accumulate below the plant, making a mat and forming a hummock of soil. Soil thin sections were prepared from the plant necromass and underlying soil to examine biological features by optical microscopy. Small organic fragments and soil aggregates were observed under a scanning electron microscope, coupled with a microprobe. C and N contents were measured, soil samples were analyzed by infrared spectroscopy and preliminary quantitative sampling of meso and macrofauna was executed in the plant residues and the underlying soil strata. Observations and analyses showed that soil microaggregates were faecal pellets from fauna, mainly Enchytraeids and Acari, living in the rooted soil below the grass. These biological aggregates exhibited a concentric internal structure and a silicon-rich coating which presumably protects them against microbial decomposition. Organic matter showed a predominance of aliphatic components upon aromatic components and appeared to be stable within the whole soil profile. As a consequence of plant die-off and mesofaunal activity, organic products accumulate and soil thickness and carbon storage increase with time. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Andosols; pedogenesis; biogenic structures; montane grassland; Mexico

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1. Introduction

Volcanic ash is known to be highly susceptible to climatic weathering and to provide favourable physical and chemical conditions for plant growth and subsequent soil development. In volcanic soils on ash materials, currently named andosols, vegetation type may have dramatic effects on pedogenic processes. Striking differences between forest and grass vegetation in relation to the type of andosol have been noticed in various regions of the world. Particularly, Japanese pampa grass *Miscanthus sinensis* has been recognized to greatly contribute to the formation of very dark humus-rich andosols classified as Melanudands (Soil Survey Staff, 1990). The *M. sinensis* grassland ecosystem produces higher amounts of organic matter from above and belowground plant residues than those of an oak tree, *Quercus serrata*, ecosystem from the same region (Shogi et al., 1990). In Alaska, secondary vegetation dominated by the grass *Calamagrostis*, growing densely on tephra deposits after forest fires, contributes to the transformation of primary Spodosol-like soils into humus-rich andosols (Shogi et al., 1988).

In the high altitude region of the Cofre de Perote volcano, Veracruz, Mexico, conspicuous carbon accumulation was observed in soils beneath pine trees and a dense herbaceous stratum of *Mulhembergia macroura* grass. The soil was a black and humus-rich andosol with a particularly high water holding capacity of 200 l of available water per square meter of soil within a depth of 1.5 m, without major variations during the year (Dubroeuq et al., 1992). This soil was essentially composed of allophane, i.e., silico-aluminous amorphous minerals, forming with organic matter a black colloidal substance. Carbon contents varied between 10 to 20% and nitrogen between 0.5 to 1.3%. From the surface to a depth of 1 m, a particularly fine 'fluffy' soil structure composed of discrete microaggregates was observed. This structure is typical of andosols and results in part from the proper arrangement of the amorphous organo-mineral compounds into elementary spheroidal particles 0.01 to 1 μm in size. Microaggregates are composed of clusters of these elementary particles (Maeda et al., 1977; Bech-Borras et al., 1977).

Preliminary field observations confirmed that the *M. macroura* grass undergoes a specific in situ decomposition. The dead leaves, in various states of decomposition, were accumulated at the base of the plant, forming a hummock of earth and organic residues upon which the green leaves were growing. The hummock was observed around all the mature individuals but not around the young ones, indicating that it was a product of plant growth which presumably involved strong interactions between soil fauna, roots and necromass. This environment is in many respects comparable to the one created by *Espeletia* sp. in the Andean paramo of Venezuela. Although dead organic residues are chiefly accumulated along the stem of *Espeletia*, they also undergo an in situ decomposition process (Monasterio and Sarmiento, 1991).

Decomposition is essentially the result of microbial activity, largely influenced by temperature and humidity. However, the soil system contains some of the richest animal communities (Anderson, 1975) which exert a direct influence on microbial activity (Couture and Fortin, 1983) and contributes significantly in the soil formation. Arthropods and earthworms were shown to have an important role in soil structure formation (Pawluk, 1987; Lee, 1985; Blanchart, 1990). Enchytraeids are also known to greatly influence soil structuring and porosity (Van Viet et al., 1993).

In most forest and grassland ecosystems, dead leaves, litter and roots are the active sites for biological decomposition and mineralization processes (Toutain, 1987; Shaw et al., 1991). In montane forest soils, where moderate temperatures prevail, microarthropods, enchytraeids and earthworms play an important role in stimulating the activity of microorganisms like bacteria, actinomycetes and fungi (Toutain et al., 1982; Bernier and Ponge, 1994). Such meso- and macroorganisms play a prominent role at the beginning and at the end of the decomposition process of organic matter from leaf litter (Lavelle et al., 1993).

This study aimed at testing the hypothesis that soil fauna (microfauna < 0.2 mm, mesofauna between 0.2 and 2 mm and macrofauna > 2 mm) linked to the necromass and the rooted soil of *M. macroura* contribute to the decomposition process and are instrumental in soil formation and subsequent carbon accumulation. The present work has been based on in situ observations of leaf residues, litter and soil at scales from 5 to 200 μm . Special attention has been paid to mesofauna, bacteria and fungi and the products of their activity.

2. Materials and methods

2.1. Location and environment

The study was located on the eastern slopes of the Cofre de Perote (Veracruz State, Mexico), a complex andesitic volcano facing the Atlantic Ocean, between altitudes of 2000 and 4000 m. (19°25'N, 97°11'W; Fig. 1). In that range of elevation, clouds pushed by northern winds are retained along the mountain sides and determine a temperate and humid climate with annual precipitation of 1800 to 2000 mm. Natural vegetation is an open pine tree forest with thick understorey layer of perennial *M. macroura* and *Stipa* sp. grass. In this region, deep black andosols predominate. This type of soil is observed in grasslands where *M. macroura* is particularly abundant.

2.2. Soil profile

The site of study has been selected in a depressed and slightly inclined 200 m² large area at 3100 m above sea level. In this zone, mean annual temperatures

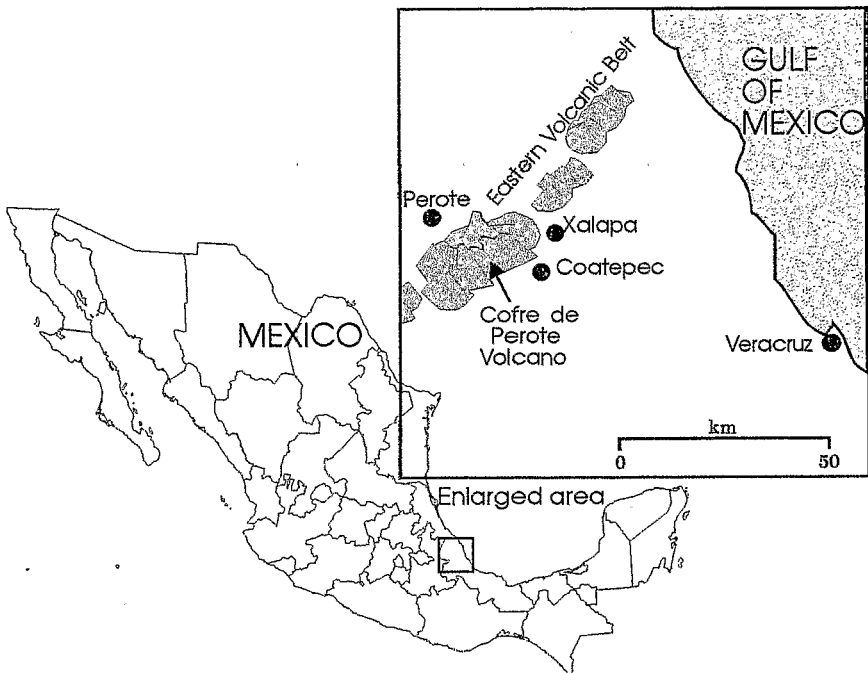


Fig. 1. Location map.

are between 5°C and 10°C with 100 to 250 frost days a year (Soto and Angulo, 1990) corresponding to a mesic (Soil Survey Staff, 1990) soil temperature regime. Soil profile comprises black allophanic horizons of about 2 m thick overlying deep brown clayey horizons and, at depth, a weathered pyroclastic ash flow with dacite blocks (Fig. 2). The black allophanic horizons have about 13% carbon (see Table 1). In these horizons, organic matter and allophane are generally bound by stable aluminium- and iron-humus complexes (Wada and Higashi, 1976). From the surface to a depth of 1.5 to 2 m, contrasted soil structures were observed in the black allophanic horizons: a well-developed microaggregate structure in the upper and middle part of the soil, a massive structure crossed by tubular voids and channels of 0.2 to 0.5 mm in diameter in the lower part of the soil (Fig. 2).

2.3. Sampling procedure

Undisturbed samples and bulk soil samples were collected vertically across a section of an individual of *M. macroura* and the soil below (Fig. 3). A set of five samples of both categories (sampling positions 1, 2, 3, 6, 7) was taken at 5 cm above the surface in the plant necromass to a depth of 60 cm in the soil, and two samples were taken at depths of 200 and 220 cm (sampling positions 8, 9), plus a sample away from the plant at a depth of 5 cm (sampling position 10).

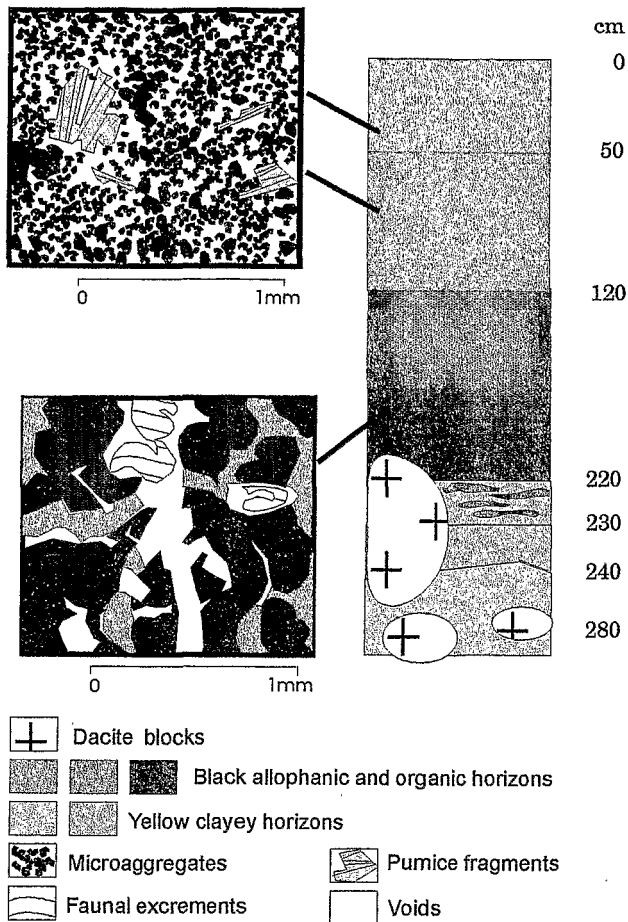


Fig. 2. Soil profile with magnified soil structure of the black allophanic horizons.

Bulk soil samples were used for physico-chemical analysis. Small fragments from the undisturbed samples were observed under a scanning electron microscope. Soil thin sections were prepared for optical microscopy from the undisturbed samples. A preliminary faunal inventory was performed on a parallel set of 4 samples from depths of 10, 20, 30 and 40 cm (sampling positions 3, 4, 5, 6) vertically below the tussock of *M. macroura*.

2.4. Physico-chemical and mineralogical analyses (see Tables 1–3)

Particle-size fractions were determined by conventional sieving for the coarse fractions and automatic procedure for clay and silt fractions after ultrasonic dispersion, using a Sedigraph 5000. Si_o , Al_o and Fe_o were extracted from amorphous hydrous oxides with 0.2 M NH_4 -oxalate solution at pH 3 (Schwertmann, 1964), Si_p , Al_p and Fe_p bonded to organic compounds were extracted by

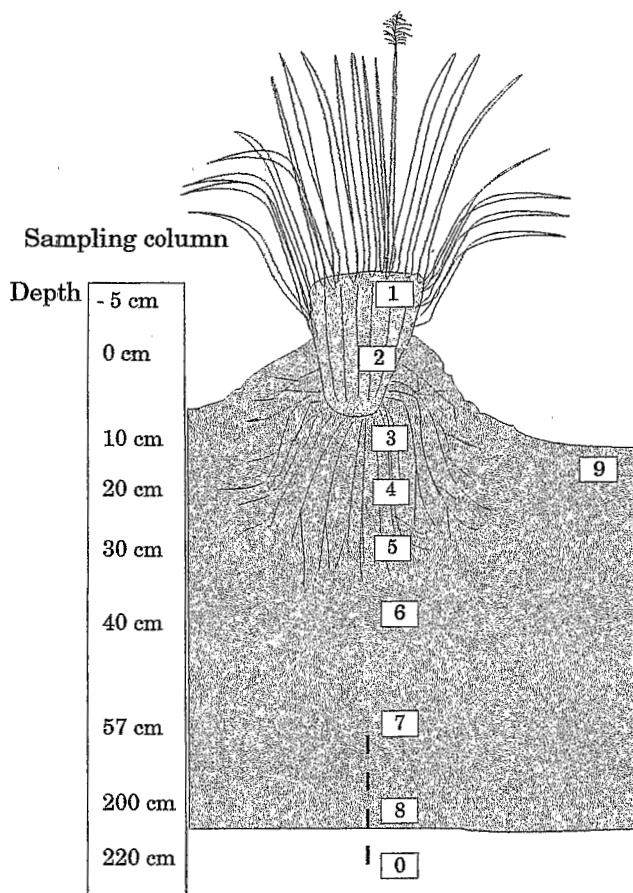


Fig. 3. Sample distribution within a cross-section of the grass and the soil below.

0.1 M Na-pyrophosphate (McKeague, 1967) and measured in the extracts by atomic absorption spectrometry. C and N contents were measured in four separate fractions of each sample, using a Carlo Erba analyser.

Four samples from the black allophanic horizons, at depths of 20, 80, 140, 210 cm, were analyzed by X-ray diffraction using a Siemens D 500 diffractometer with Cu anticathode. In order to compare the clay fraction with the whole soil material, a set of 4 bulk soil samples and a set of 4 clay samples were processed separately. Clay fraction was obtained by ultrasonic dispersion and sedimentation after a treatment with 30% H_2O_2 and NaOAc buffer solution (pH 5) to remove all the organic matter.

IR spectroscopy was performed on 8 samples including plant necromass and soil. The dried samples were refrigerated at 4°C in acetone and mechanically ground to less than 2 μm , the particle size of the samples having to be smaller than the IR wavelength used for quantitative estimations. Each sample was

Table 1

Average values of C and N contents from 4 replicates of each sample, in dry g kg⁻¹

Sample no.	Depth (cm)	C	N	OM	C/N
1	-5	180.8	11.2	311.7	16.1
2	0	197.9	12.9	341.2	15.3
10	5	137.7	9.1	237.4	15.0
3	10	143.2	9.7	246.9	14.8
6	40	118.6	7.7	204.4	15.3
7	57	98.8	6.4	170.3	15.3
8	200	96.1	6.0	156.7	16.0
9	220	140.7	8.8	242.6	15.9

mixed by hand with KBr for preparation of pellets. Fourier transform infrared (FT-IR) spectra were recorded on a Perkin-Elmer FT 16 PC spectrometer in the 4000–250 cm⁻¹ wavenumber range with a 2 cm⁻¹ resolution. Peak height was calculated from absorbance band intensities. The base line chosen for band intensity measurement was the valley-to-valley line.

2.5. Fauna inventory

A simplified sampling of the fauna was accomplished in the same plant and underlying soil as the one that has been studied by microscopy and IR spectroscopy. One sample of 1 l was taken from four soil layers at depths of 10, 20, 30 and 40 cm. The fauna was extracted by mixing each sample in water and sieving through two sieves of 0.979 mm and 0.489 mm mesh size, respectively. All the recovered material was fixed in 70% ethanol, identified and counted under stereomicroscope. All the individuals were identified at the level of orders or families and then they were counted and weighed to evaluate the biomass of each meso and macrofaunal group. Although this method largely underestimates nematode and enchytraeid densities it allows valuable comparisons among different soil strata.

Table 2

Exchangeable acidity and pH

Depth (cm)	cmol(+)/kg			pH	
	1 N KCl exchangeable		NH ₄ OAc extract.	H ₂ O	KCl
	H	Al	Al		
20	1.47	1.20	13.12	4.68	4.55
80	0.138	0.097	13.12	5.30	5.26
140	0.598	0.485	15.79	5.09	4.67
210	0.092	0.019	11.12	5.13	5.50
240	0.138	0.050	6.67	5.51	5.34

Table 3
Active Al, Fe and Si and allophane contents

Depth (cm)	g kg ⁻¹ (dry 105°C)						Allophane	Al _p /Al _o	C/Al _p
	0.2 M acid oxalate extract			0.1 M Na-pyrophosphate extract					
	Si	Fe	Al	Si	Fe	Al			
20	5.0	7.5	25.9	0.65	6.0	13.2	37.6	0.51	8.94
80	16.9	9.2	54.5	0.21	2.8	9.0	125.2	0.16	10.97
140	15.7	12.6	57.1	0.26	9.0	14.3	116.3	0.25	8.76
210	19.6	6.1	58.8	0.05	5.2	9.0	144.9	0.15	10.67

Al_p = Al from Na-pyrophosphate extract. Al_o = Al from acid oxalate extract.

2.6. Micromorphological observations

Soil microstructure and biological features such as arthropod faecal pellets, earthworm casts and galleries were observed in thin sections using a current petrographic microscope. Thin sections of 2.5×3 cm large and $30 \mu\text{m}$ thick were made from undisturbed soil samples impregnated in polyester resin.

Surface morphology and qualitative mineral composition of the microaggregates and necromass fragments were studied under a scanning electron microscope (SEM) Cambridge Stereoscan 200 equipped with an energy dispersive X-ray analyser (EDXA). Small undisturbed fragments no larger than 2 mm were fixed on adhesive carbon film. They were gold-coated for obtaining sharp images, or carbon-coated for qualitative analyses.

3. Results

3.1. Soil mineralogy

3.1.1. X-ray diffraction

X-ray diagrams of the raw samples from depths of 20 to 210 cm displayed major peaks corresponding to feldspars, small peaks corresponding to quartz and a pronounced bulge of the base line. No peaks attributable to halloysite clay were detected (1 and 0.445 nm).

No peaks were detected in the X-ray diagrams of the clay fraction (particle size $< 2 \mu\text{m}$) from the same samples after elimination of the organic matter. The substance appeared as noncrystalline and X-ray diagrams displayed only a large shoulder centred on 0.380 nm which was attributed to allophane (Fig. 4).

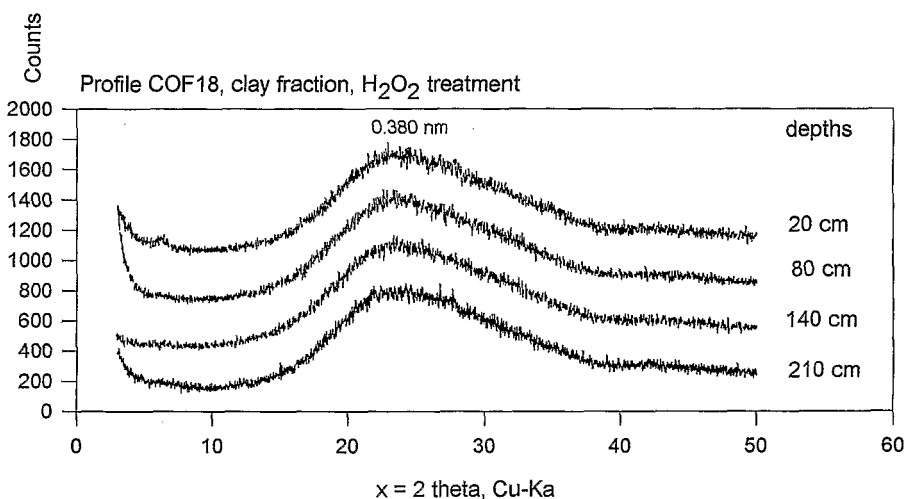


Fig. 4. X-ray diffractograms of the $< 2 \mu\text{m}$ soil fraction after H₂O₂ treatment. The large bulge centred on 0.380 nm is attributed to allophane.

3.1.2. Infrared spectroscopy

FTIR spectroscopy can be used as a quantitative method, provided the amount of absorbed radiation is proportional to the quantity of absorbing matter in the sample. For solids, a good approximation of band intensities of recognized minerals and organic groups in IR spectra (Table 4) allows a preliminary evaluation of these components in the soil.

In the wavenumber region of 1500 to 4000 cm^{-1} , the spectra showed close resemblances to a hemic peat type (Durig et al., 1988). The most clearly defined bands related to organic compounds were 2926 cm^{-1} (aliphatic C–H stretching), 1715 cm^{-1} (C=O stretching of carboxylic acids), 1457 cm^{-1} (CH_2 – CH_3 groups), 1390 cm^{-1} (CH_3 groups). Absorption bands of aromatic compounds were very reduced or not represented (1457 and 1510 cm^{-1}). The 1030 cm^{-1} (C–O–C stretch) and 1070 cm^{-1} (C–OH stretch) which are two strong bands of cellulose and hemicellulose (Blackwell, 1977) were not detected, probably because large absorption bands of allophane prevailed in this region or cellulose was entirely decomposed (Fig. 5).

Apart from the two wide bands centred on 3400 cm^{-1} and 1650 cm^{-1} and attributed to O–H stretching vibrations of either structural OH groups or adsorbed water and of the H–O–H deformation vibration of adsorbed water, respectively, the main absorption band of allophane compounds is in the 940 to 1040 cm^{-1} region (Wada, 1977; Parfitt and Henmi, 1980; Quantin, 1992). It is related to the stretching of Si–O–Al in the 900–970 cm^{-1} band and the stretching of Si–O bonding in the 1020–1040 cm^{-1} band. The position of the main absorption band toward the large wavenumbers is an indicator of higher Si/Al molar ratios (Wada, 1977). Pure silicon gels should have a 970 cm^{-1} band (Bartoli, 1981). Since this band was not observed in the samples all the amorphous compounds were silico-aluminous. The 800 cm^{-1} band (symmetrical Si–O–Si) and the 1090 cm^{-1} band (asymmetrical Si–O–Si) are attributed to

Table 4
Calculated peak height of characteristic absorbance bands in the FTIR spectra

Sample no.	Halloysite	Gibbsite	CH–CH	C = O	CH ₂ –CH ₃	CH ₃	Si–O–Si	Quartz
	Band cm^{-1}							
	3698	3450	2926	1715	1457	1385	1385	779
1	0.0080	0.0168	0.0554	0	0.0385	0.0596	0.0562	0.0071
2	0.0007	0.0096	0.1385	0.0045	0.0422	0.0433	0.0477	0.0299
3	0.0009	0	0.0283	0	0.0275	0.0431	0.0701	0.0476
6	0	0	0.0307	0	0.0280	0.0416	0.0637	0.0516
7	0	0	0.0208	0	0.0097	0.0307	0.0802	0.0545
9	0.0023	0.0346	0.0522	0	0.0314	0.0483	0.0476	0.0235
8	0.0065	0.0113	0.0287	0	0.0442	0.0575	0.0245	0.0135
10	0.0031	0.0186	0.0765	0	0.0468	0.0525	0.0508	0.0311

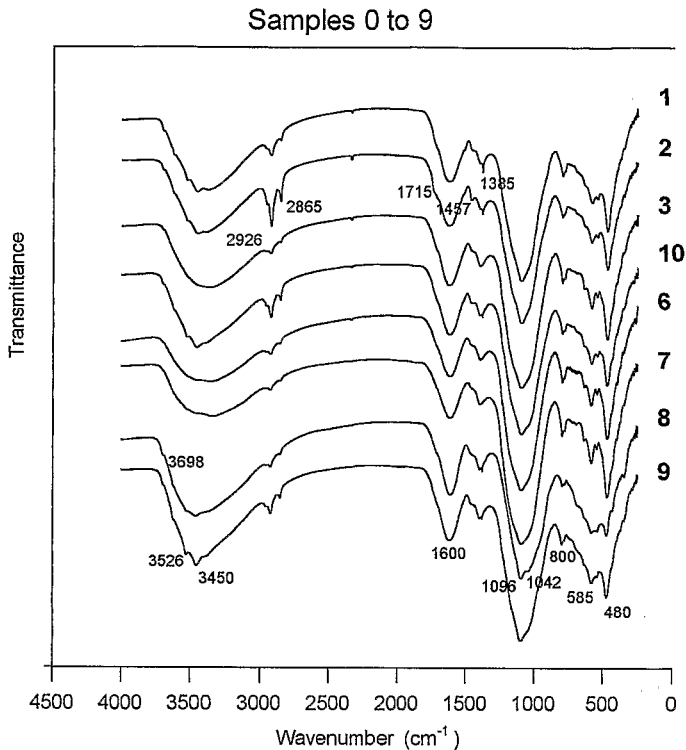


Fig. 5. IR spectra of the soil samples were similar from the soil surface to depth except in the two samples from the necromass where the aliphatic compounds bands (2926 and 2865 cm^{-1}) were more intense than in the underlying soil samples.

an amorphous silica phase (Farmer et al., 1979; Webb and Finlayson, 1987), probably from opaline silica or phytolithes. In samples 8 and 9, the position of the main absorption band at 1040 cm^{-1} , together with a large band near 575 – 590 cm^{-1} related to the stretching of Al–OH bondings, is interpreted as Si-rich allophane (Van den Marel and Beutelspacher, 1976; Farmer et al., 1979).

Small secondary bands were detected at 3450 cm^{-1} (Gibbsite) and 3526 – 3698 cm^{-1} (Halloysite) indicating only traces of these minerals, except for a higher gibbsite content in sample 9 (Fig. 5).

The presence of dominantly Si–allophane and amorphous silica are indicators of a global enrichment of Si. This enrichment may be explained by a biological input of silica to the soil from phytolithes which are abundant under grass vegetation.

3.2. Carbon and nitrogen contents in the soil

The C/N ratios in the whole soil profile had a relatively constant value near 15, except in the plant necromass and below a depth of 40 cm in the soil where the values were above 16 (see Table 1).

3.3. Soil composition

The soil is mainly composed of allophane and organic matter. OM contents estimated from C contents were about 24% (Table 1). Allophane contents estimated from Al-oxalate extract were about 12 to 14% (Table 3). As shown by Saigusa et al. (1991), the Al_p/Al_0 ratio < 0.5 indicates that the soil is an allophanic andosol (Table 3). Halloysite clay was detected only as traces. Gibbsite was discernible only in small amounts in the lower horizon (sample 0). With respect to organic matter, two points are evident: (1) aliphatic compounds are more predominant than aromatic compounds; (2) IR spectra are quite similar from the plant necromass to a depth of 200 cm in the soil.

3.4. Biological activity in the necromass and in the soil

3.4.1. Optical microscopy observations

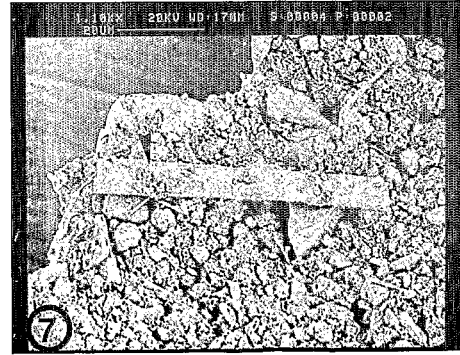
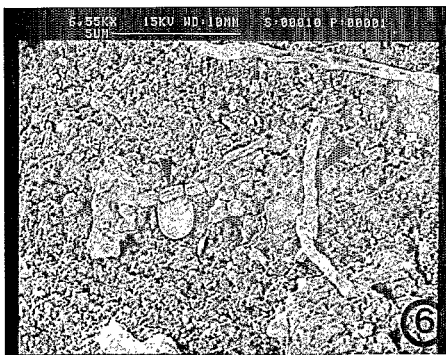
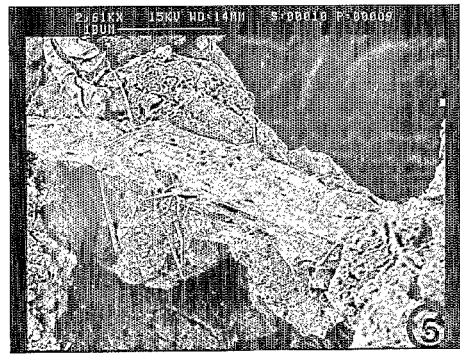
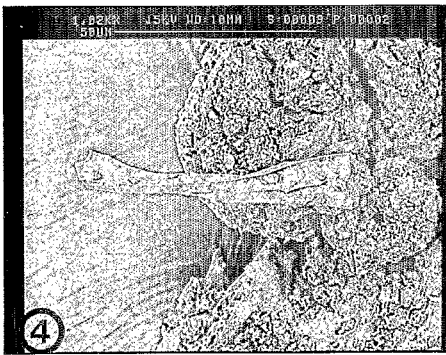
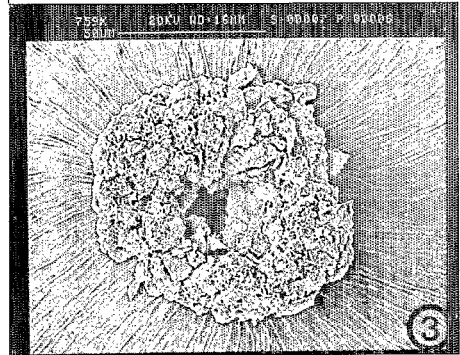
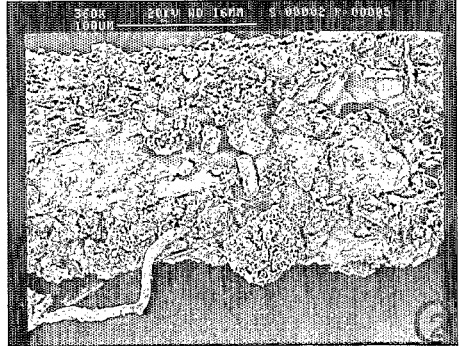
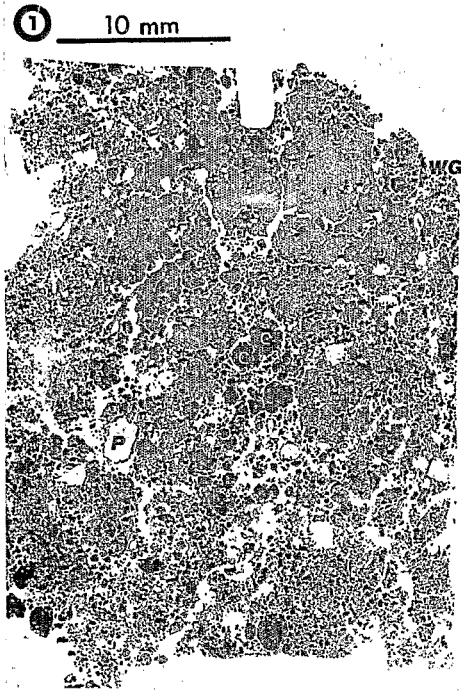
General microstructure is a crumb structure composed of more or less rounded, rugose, 6×3 mm to 10×7 mm large aggregates that are not accommodating each other and are composed of small granules partially welded together. From the necromass to a depth of 57 cm the recognizable organic fragments decreased in quantity with depth. Conversely, pumice shards increased with depth, in quantity and in size. There were also more pieces of pure carbon with recognizable root structure in the deepest layers, probably remnants of ancient tree roots.

In samples 1 and 2, the organo-mineral aggregates were denser, blacker and richer in humified organic matter than in the underlying soil samples. Close to the vegetal debris, rounded humified particles about $70 \mu\text{m}$ in diameter were abundant. They were probably excrements from acari or small enchytraeids. In sample 7, at a depth of 57 cm, larger and more compact aggregates of 0.1 to 0.2 mm in size (Fig. 6(1)) could be faecal pellets of enchytraeids or of small earthworms. Other features of biological activity were galleries infilled with less compact soil and a chamber of 2 mm in width, lined with a 0.3 mm thick, organic-rich coating, darker than the rest of the material (Fig. 6(1)).

3.4.2. SEM observations

Plant debris appeared to be coated with hydrated, organic and noncrystalline material (Fig. 6(2)). Part of this material was distributed into rounded, 50 to

Fig. 6. (1) Soil thin section from sample 7 at a depth of 57 cm under *M. macroura* grass. C: earthworm casts, G: gallery, GW: gallery wall. (2) Vegetal debris in process of decomposition with aggregates of humified organic matter (sample 2). (3) microaggregate with a hollow center and concentric layers (sample 7). (4) microaggregate with polished surface (sample 9). (5) Mycelial strand of fungi on organic matter (sample 2). (6) Bacteria (arrow) on nonaggregated organic matter (sample 1). (7) Phytolithe (arrow) constituted of amorphous silica (sample 1).



100 μm large aggregates, of the same size as those observed in thin sections. These aggregates were probably faecal pellets of the mesofauna. Some of them, more or less fragmented, exhibited a hollow centre and concentric internal layers (Fig. 6(3)). This concentric structure typically reflects the biological origin of the pellets, probably from the gut of organisms like Acari. Others rounded aggregates exhibited a polished, silicon-rich surface (Fig. 6(4)). These casts were attributed to *Enchytraeidae*, and this surface coating was probably intestinal mucus (Blanchart et al., 1993).

In the deepest strata, aggregate size became more heterogeneous and a new group of 100 to 200 μm large aggregates was coexisting with the small aggregates, and appeared to be a mixture of organo-mineral materials in which vegetal fragments were no more discernible.

In the whole profile, other features of intense biological activity were observable such as mycelial strand of fungi (Fig. 6(5)), bacteria on vegetal residues (Fig. 6(6)), protozoa and parts of acari exoskeleton. Mineral fragments were essentially phytolithes (Fig. 6(7)), i.e., amorphous silica residues from grass, and glass shards from tephra. Commonly observed in the surface samples, the mineral fragments tended to disappear in the deepest soil strata.

3.5. Soil fauna

3.5.1. Composition

Ten meso- and macrofauna groups were found, which comprised Oligochaeta (*Enchytraeidae* and *Megascolecidae*), Nematoda, Acari, Chilopoda, Symphyla, Homoptera, Coleoptera, Diptera and Hymenoptera. *Enchytraeidae* was the most

Table 5
Meso- and macrofaunistic groups under *M. macroura* grass

Groups	Depth (cm)			
	0–10	10–20	20–30	30–40
Oligochaeta enchytraeidae	17	61	19	25
Nematoda	14	20	8	19
Acari	17	37	1	2
Coleoptera (larvae)	3	1	4	2
Coleoptera	5	3	1	1
Chilopoda	2	4	0	0
Diplopoda	2	1	0	0
Oligochaeta megascolecidae	0	0	0	3
Homoptera	0	1	0	1
Hymenoptera	0	1	0	0
Diptera	0	1	0	0
Symphyla	0	1	0	0

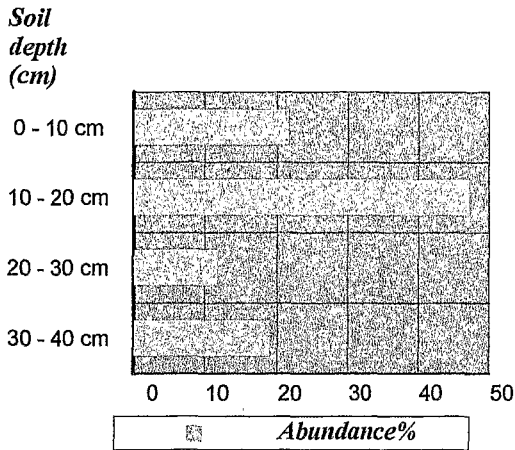


Fig. 7. Proportional vertical distribution of the soil fauna.

abundant group representing 44% of the animals, followed by Nematoda (22%) and Acari (20.5%). Total density of organisms was 277 individuals per dm^2 or 27 700 per m^2 (Table 5).

3.5.2. Vertical distribution

Considering the method of quantification, non-selective for nematodes and enchytraeids, the present data of population can be used only as comparisons between the different soil strata. The stratum 10–20 cm, the most densely rooted soil volume, is the richest in organisms. The stratum 20–30 cm is the poorest. This pattern also holds for the main groups separately at different soil depths (Fig. 7).

The soil structure is highly influenced by *Enchytraeidae*. Although the quantification method was clearly inadequate for this group, a biomass of approx. 1220 mg (dry weight) per m^2 was measured, which was probably inferior to the real population. Most of the aggregates corresponded to the size of the casts of these organisms (Gelder, 1984 in Didden, 1993; Pawluk, 1987).

4. Interpretation and discussion

Results obtained from infrared spectroscopy confirmed that the organic matter stored within the soil is similar to the organic matter recently produced in the necromass by biological activity. Constantly large C/N ratios in the soil and in the litter are also a criterion for organic matter stability. In these conditions the fate of the humus, produced in the litter from vegetal tissues by decomposers, is oriented more towards accumulation in the soil than towards mineralization.

FTIR spectra indicate that this organic matter is rich in aliphatic compounds and is in many points comparable to an hemic peat type in which cellulose decomposition should be achieved. This type of organic matter is apparently very different from that of the dark coloured andosols under grassland vegetation in Japan (Nanzyo et al., 1993), classified as Melanudands (Soil Survey Staff, 1990) and in which prevail humic acids rich in carboxyl–carbonyl groups and aromatic rings. These results tend to indicate that environment and soil evolution are not the same as those of the Melanudands in Japan. However, this point cannot be resolved in the present study. To determine the exact composition of the organic material would require further separations of humic acids into different types, according to their relative colour intensity.

The close relation observed between the grassland with *M. macroura* and the underlying humus-rich andosol raises questions about the origin of the carbon accumulated in the soil: is the grass an efficient carbon supplier? Through a three year capture of the above-ground green leaves and residues in a plot with four individuals of *M. macroura* (Table 6), an approximation of the mean annual C input per m² estimated from the plant residues was 143.3 g. This carbon contribution from vegetal residues is not specially high. Therefore, carbon accumulation presumably results not only from humification of vegetal residues but also from a blockage in the mineralization process.

The predominance of enchytraeids in the soil fauna is in many respects comparable to soils from cold ecosystems like tundra or coniferous forests (Dash, 1990). In the high-altitude grasslands with *M. macroura*, enchytraeids ensure the homogenization of the soil strata by their constant migration inside and outside the rhizosphere (Didden, 1993). These organisms contribute also to the stability of the soil material by formation of spherical casts with a silicon-rich cortex which is presumably a physical protection against water and bacterial decomposition. This cortex is supposed to have formed from intestinal mucus. In addition to biological protection of the soil microstructure, the relative resistance of aluminium–allophane complexes to biodegradation (Wada and Higashi, 1976; Boudot, 1992) and the temporarily low temperatures bring about severe constraints on the biodegradation process.

Table 6

Estimates of C and N inputs from above-ground litter and green leaves collected annually on a 4 m² plot with 4 plants of *M. macroura* grass

Sampling date	Dry matter (g)		Carbon (g)		Nitrogen (g)	
	Litter	Green leaves	Litter	Green leaves	Litter	Green leaves
December 1992	914.1	884.2	488.1	413.8		
March 1993	698.8	74.3	344.5	36.4	5.93	0.56
June 1994	739.9	120.4	378.8	59.4	6.31	0.91
Average (y ⁻¹ m ⁻²)	196.1	89.9	100.9	42.4	1.53	0.18

5. Conclusion

(1) Microaggregates are built by the soil fauna. They are essentially faecal pellets and excrements of three size classes: large (> 0.5 cm), medium (100–200 μm), small (50–100 μm). Medium and small aggregates are protected by a gel-like silicon-rich coating.

(2) The greatest faunal abundance is observed in the zone of the most intense rooting of *M. macroura*. Here, enchytraeids, acari and nematodes predominate. The presence of earthworms collected in the deeper strata (40–60 cm) is correlated with the observation of large aggregates in this part of the soil.

(3) Organic matter appears to be composed mainly of aliphatic compounds, probably from the decomposition of hemicellulose and cellulose-rich residues.

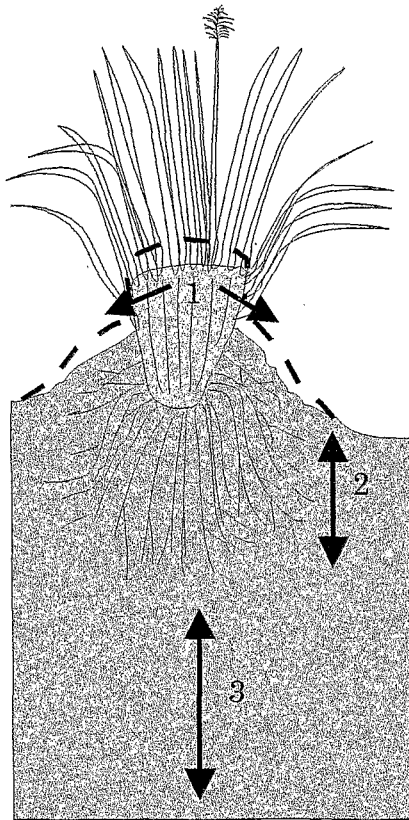


Fig. 8. Interpretative model of the soil formation under the perennial grass *M. macroura*: (1) active bacterial and fungal decomposition produces a necromass; (2) abundant mesofauna located in the rooted soil produces stable microaggregates inducing an elevation of the soil surface around the plant; (3) macrofauna homogenizes the microaggregates into bigger aggregates in the underlying soil strata.

Decomposition products appear to be stable and accumulate in the soil without undergoing further decomposition. This stability presumably results from both the soil structure, as spherical microaggregates with a protective coating, and the soil material itself, made of allophane bonded to stable aluminium/iron–humus complexes.

Given these three findings, an interpretation for soil formation through interacting plant growth and faunal activity in *M. macroura* grassland environment is presented in Fig. 8. In the aerial part of the plant, decomposition of vegetal tissues by bacteria and fungi is very active in the leaves at the base of the plant. The young leaves grow upon the necromass at the topmost part of the plant and contribute to increase the height of the tussock. In the rooting zone, active mesofauna produces stable microaggregates which accumulate under and around the base of the plant, forming a hummock of earth. In the lower soil stratum we suppose that earthworms play an important role in transporting organic matter from soil surface to depth and in homogenizing the soil material into larger aggregates.

The result is the formation of recent organic soil layers that superimpose upon old layers, leading to an increasing soil thickness and carbon accumulation.

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Volcanic Ash Soils

Genesis, Properties and Utilization

by S. Shoji, M. Nanzyo and R.A. Dahlgren

Developments in Soil Science Volume 21

Volcanic eruptions are generally viewed as agents of destruction, yet they provide the parent materials from which some of the most productive soils in the world are formed. The high productivity results from a combination of unique physical, chemical and mineralogical properties. The importance and uniqueness of volcanic ash soils are exemplified by the recent establishment of the Andisol soil order in Soil Taxonomy. This book provides the first comprehensive synthesis of all aspects of volcanic ash soils in a single volume. It contains in-depth coverage of important topics including terminology, morphology, genesis, classification, mineralogy, chemistry, physical properties, productivity and utilization. A wealth of data (37 tables, 81 figures, and Appendix) mainly from the Tohoku University Andisol Data

Base is used to illustrate major concepts. Twelve color plates provide a valuable visual-aid and complement the text description of the world-wide distribution for volcanic ash soils. This volume will serve as a valuable reference for soil scientists, plant scientists, ecologists and geochemists interested in biogeochemical processes occurring in soils derived from volcanic ejecta.

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