

Provided for non-commercial research and educational use only.
Not for reproduction or distribution or commercial use.



This article was originally published in a journal published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues that you know, and providing a copy to your institution's administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

Original article

Influence of some physicochemical and biological parameters on soil structure formation in alluvial soils

Géraldine Bullinger-Weber^{a,*}, Renée-Claire Le Bayon^a,
Claire Guenat^b, Jean-Michel Gobat^a

^a *Laboratory Soil and Vegetation, University of Neuchâtel, Emile-Argand 11, Mailbox 158, CH-2009 Neuchâtel, Switzerland*

^b *ISTE-pédologie, Ecole Polytechnique Fédérale de Lausanne, 1015 Lausanne, Switzerland*

Received 4 August 2005; accepted 10 May 2006

Available online 30 August 2006

Abstract

This study examines the role of abiotic (texture, calcium carbonates or iron) and biotic parameters (earthworm and enchytraeid activities) on the initial phases of soil aggregation. Our research focused on humus forms in alluvial soils, which are considered as young and heterogeneous environments. We hypothesized that the soil structure formation is determined by both the nature of the recent alluvial deposits and the soil fauna. For this purpose, six sites were chosen throughout two types of softwood forests (willow and alder forest) representing two stages of vegetation succession. Evidence of soil texture influence on aggregate stability was observed. A dominance of a coarse sand fraction caused a quick colonization of enchytraeids and epigeic earthworms while a silty texture favoured the presence of anecic earthworms, thus increasing the aggregate stabilisation. Iron forms, acting as cementing agents, were observed in the coarse silt, while calcium carbonates were equally distributed among the textural fractions. Active calcium carbonate fraction, binding organic matter with mineral components, was not found in the coarse sand fraction. In conclusion, the tree age cannot alone be used as an indicator of the humus form evolution but biological and physicochemical parameters also influence the initial steps of soil structuration.

© 2006 Elsevier Masson SAS. All rights reserved.

Keywords: Soil aggregate stability; Earthworms; Enchytraeids; Physicochemical factors; Humus form; Alluvial soil; Softwood forest

1. Introduction

Soil structure is influenced by different properties of the soil constituents and by its environment [11]. Soil aggregation is related to basic soil properties such as the texture and the type of parental material. The amount of clay, as well as the presence of calcium carbonates

and iron acting as cementing material, influences the aggregate formation and stabilisation [21]. Soil carbonates usually work as a source of Ca^{2+} -ions that help to flocculate clay particles and then stabilize the exchange complex. Moreover, calcium carbonates preserve the flocculated structure of the clay in soil surface aggregates by neutralizing acids produced by fungi, microbes and roots. A high content of iron oxides also favours a stable structure and may be more concentrated in the fine clay particles. But Oades [35] also found that in temperate regions the interactions of oxides with clays may

* Corresponding author. Tel.: +41 32 718 2220; fax: +41 32 718 2231.

E-mail address: geraldine.bullinger@unine.ch (G. Bullinger-Weber).

be reversed in the presence of humic substances and that the contribution of these iron oxides is often difficult to separate from the stability attributable to organic matter. As a matter of fact, organic matter is an important factor in soil aggregation, which is correlated with the organic carbon content [53]. Soil organic matter is assumed to stabilize aggregates against disruptive processes such as slaking, by increasing the cohesion of aggregates through the binding of mineral particles by organic polymers. It could also decrease the wettability of aggregates, thus reducing their rates of wetting and the extent of slaking [12]. Organic substances are very repellent to water and several organic fractions are responsible for this hydrophobicity of soils, e.g. humic acids, aliphatic fractions or plant litter debris.

Soil aggregate formation is not only determined by the physical or chemical properties of the soil, but also by soil biological processes. Soil biota is numerous and diverse and is mainly represented by earthworms (macrofauna), enchytraeids, collembolans, diplopoda (mesofauna), nematodes, rotifers (microfauna), as well as fungi and bacteria (microflora). Living organisms, especially worms (Oligochaeta), play a major role in soil structure. For instance, the action of enchytraeids contributes to litter degradation and nutrient mobilization, particularly in acid soils with a high organic content [5,32,47,55]. In addition, soil bioturbation by earthworms is essential and produces very stable casts as well as a large burrow network [36,49]. Earthworms affect soil physical properties by ingesting and egesting soil, but their effects on soil aggregation is species specific and depends on their ecological strategy [49]. While epigeic individuals feed mainly on organic matter, the material ingested by endogeic and anecic species is mainly mineral matter, which is mixed with organic matter in digestive tracts and then egested as casts on the soil surface or belowground. The quality of the ingested material, as well as the contribution of earthworms to cast production and aggregation are well documented [13,22,33,49]. Furthermore, Marinissen and van den Bosch [31] proposed a simple model on the colonization of new habitats by earthworms such as grasslands, while Zorn et al. [57] examined the earthworm population dynamics in a floodplain system in relation to frequency and duration of flooding events. However, the colonization of young environments by different worm species and the first interactions between mineral and organic materials under the influence of soil fauna in the upper soil layers are not well known, particularly in the first steps of soil formation and aggregation.

At the top of soil profiles, humus forms function as the habitat of decomposer organisms and as a nutrient

sink and source [27]. These properties are reflected in morphological characteristics of humus form horizons manifested by the mode and the rate of decomposition and they can then be defined as a morphological pattern observed in the association of organic and mineral matter. It has been demonstrated that humus forms play a central role in the functional biodiversity of terrestrial ecosystems. Actually they are stable and display a visible result of the activity of the soil animal and microbial life [41]. Moreover, small-scale variations in the topsoil profile composition may occur under the influence of several conditions such as vegetation, soil properties or microtopography [39]. Humus forms can then be considered as excellent tools to investigate the first interactions between mineral and organic materials under colonizing fauna.

Alluvial soils have already been described as reliable models to detect the influence of both abiotic and biotic mechanisms involved in soil structure [23]. They are considered as young soils depending on a complicated genesis (interaction between inheritance and in situ evolution) and situated in a heterogeneous environment (i.e. herbaceous vegetation, tree population, alluvium) where early stages of soil formation are represented.

As a consequence, we studied alluvial soils to investigate the relative importance of abiotic (texture, different types of carbonate and iron forms, organic matter) and biotic (enchytraeids and earthworms) mechanisms on initial soil aggregation. Our research focused on the humus form, which is considered as a good indicator of short-term and small-scale variations under the influence of vegetation or sedimentation changes. We hypothesized that the soil structure formation was mainly determined by the nature of the recent alluvial deposits with little influence of alluvial gravel or underlying mineral sediments. This upper mineral part, directly in contact with organic matter, affects in turn the colonization by the soil fauna (earthworms and enchytraeids), and the distribution of the different iron forms, with little influence of the forest types that are, in our case, pioneer communities of willow and alder. We concentrated our study on six sampling sites differentiated mainly by recent alluvial deposits and by the age of the tree populations. Alluvial gravel as well as other underlying mineral horizons were considered as similar for the six sites. We characterized these soils biologically, chemically and physically and observed that the spatial distribution of humus forms throughout the alluvial study area was very heterogeneous, regarding earthworms (abundance, biomass and species), enchytraeids, soil textural parameter and iron forms.

2. Material and methods

2.1. Site description and sampling method

The study site is an alluvial zone of national importance (Fig. 1) located in the northwest of the Swiss Alps (Swiss coordinate system in km: 571.5/154). It is a part of the floodplain of the Sarine River, tributary of the Aare River. The Sarine River is strongly confined between embankments except for the study area situated at 750 m above the sea level [9,23].

Our study was based on the comparison of humus forms of six sites located on a riverbank that can potentially be flooded. These sites were selected along a transect according to the vegetation type, the age of the present tree population [23], and the visual heterogeneity of alluvial deposition. Two different types of softwood forest community were chosen with three sites in each type (Fig. 1) representing two stages of

vegetation succession in alluvial ecosystems [40]: the willow type, old gravel bars that have been colonized by willow shrubs for about 20 years (H1 to H3), and the alder type, colonized for about 25 to 30 years (H4 to H6). Inside each vegetation type, sites were chosen according to the environment heterogeneity (herbaceous plants, soil texture, etc.).

Soils were FLUVIOSOL TYPIQUE according to the “Référentiel pédologique” [1]. The humus profile of each location was described using the classification system of the “Référentiel pédologique” [1]. From each profile, the organo-mineral layers A and/or J and the mineral horizons M were sampled for further analyses.

2.2. Soil fauna extraction

Enchytraeids were sampled from three plots of 25 × 25 cm inside whose three soil cores (6 cm diameter × 10 cm deep) were mixed together. Sampling was

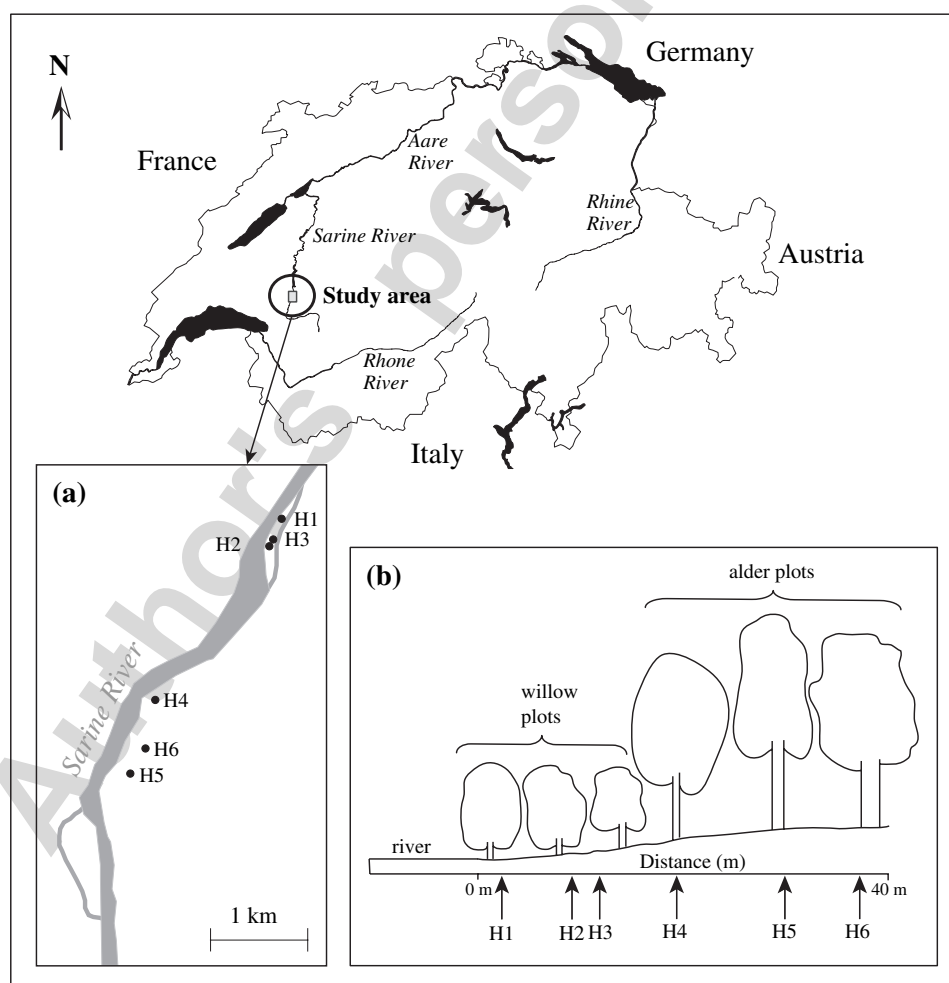


Fig. 1. The study area, the Sarine River, in the northwest of the Swiss Alps, with the location of the six sites along the river (a). (b) Schematic drawing of the Sarine River in the studied section with two stages of vegetation succession in alluvial ecosystems.

made only one time in August during and after a fairly dry period. Counting was performed after extraction using the wet funnel technique [16,37]. Earthworms were sampled from each soil (three squares of 50 × 50 cm) using the ethophysical method [8]. Sampling was realized only one time in September and October after a relative dry summer combining a formalin extraction followed by hand-sorting (soil depth 0–20 cm). All worms were weighed and identified to the species level. Small and/or juvenile individuals were classified either in their ecological type (anecic, endogeic or epigeic) or at the genus level. No major flooding event took place during the months before sampling, thus we suppose that flooding did not influence our sampled area.

2.3. Soil analysis

Samples for soil analysis were taken in May and June and at a different place than those for fauna extraction to avoid perturbing the soil communities. Physico-chemical analyses were performed on air-dried and sieved soil (mesh size 2 mm) from the layers A and/or J and M. Water pH (ratio 1:2.5), particle size distribution (modified Robinson pipette method for: fine silts 2–20 μm, coarse silts 20–50 μm, clays 0–2 μm; and sieving for: fine sands 50–200 μm, coarse sands 200–2000 μm [38]), and active carbonate content (modified Drouineau and Galet method [54]) were measured. Other analyses were carried out on ground soil samples (soil particles <200 μm), like carbonate content (reaction with H₃PO₄ and titration of the CO₂ released with a Carmograph Wösthoff 8-ADG), organic carbon content (combustion and titration of the CO₂ released with a Carmograph Wösthoff 8-ADG), and total nitrogen content (Kjeldahl mineralization, Technicon colorimetric titration). In addition, and only for A and/or J horizons, iron forms were quantified as amorphous iron species (Fe_o; iron extractable by oxalate using Tamm method modified by Schwertmann [52]), crystallized iron species (Fe_d; iron extractable by dithionite-citrate-bicarbonate modified from Mehra and Jackson method [34]) and total iron content (Fe_t; metaborate fusion method [45]). In general, Fe_o is considered as “active”, Fe_d minus Fe_o ratio as “less active” [4], and Fe_o/Fe_d ratio estimates the degree of the soil evolution [18]. Three replicates were carried out for the quantification of iron forms while one measurement was made with other methods.

Aggregate stability was determined on A and/or J horizons by wet sieving using 1.00, 0.50 and 0.25 mm mesh sizes (method adapted from Kemper and Rosenau

[26]) on 1–2 mm calibrated aggregates. The mean weight diameter (MWD) was calculated on three replicates per soil using a correction index for the coarse sand content [2].

2.4. Statistical analysis

Statistical analyses were performed using Pearson correlations and principal component analysis (PCA). The data were previously standardized to make the variance more homogeneous across the range of the data. The software used was R (version 2.0.1 [24]). Earthworm data were grouped in ecological categories before statistical analysis.

3. Results

3.1. Humus forms

Three humus forms were observed and described in the transect (Table 1, Fig. 2): eumull for H1, H2, H3 and

Table 1
Site descriptions according to the “Référentiel pédologique” [1] and thickness of each horizon

Sites	Humus forms	Horizons	Thickness (cm)
H1	Eumull	(OLn)	0.5
		J _{Sca}	1
		M _{ca}	14
H2	Eumull	(OLn)	0.5
		J _{Sca}	0.5
		M _{ca}	8.5
H3	Eumull	(OLn)	0.5
		A _{ca}	5
		M _{ca}	11
H4	Oligomull	OLn	0.5
		(OFr)	0.5
		A _{ca}	5.5
		M _{ca}	12
H5	Eumull	OLn	0.5
		(OLt)	0.5
		A _{ca}	7
		M _{ca}	3
		IIM _{ca}	10
H6	Dysmull	OLn	1
		OFr	0.5
		(OFm)	1
		J _{Sca}	7
		M _{ca}	8
		IIM _{ca}	2

The suffix “ca” underlines the presence of carbonates.

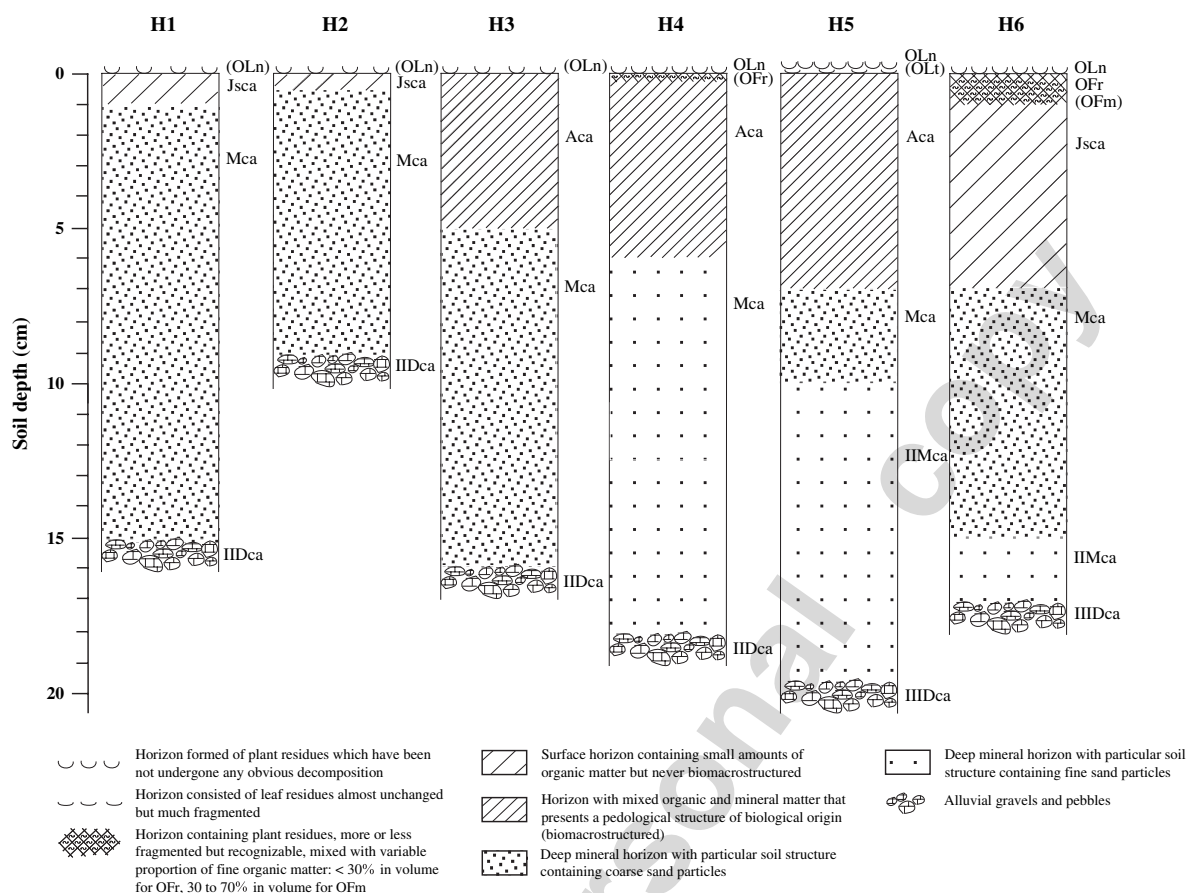


Fig. 2. Schematic diagram of the six sites. OLn, horizon formed of plant residues which have not undergone any obvious decomposition; OLv, horizon formed of plant residues which show little fragmentation, but have clearly been altered since falling to the ground; OFr, horizon consisting of easily identifiable leaf fragments which are more or less fragmented with a small proportion of fine organic matter; OFm, horizon containing equal quantities of fragmented leaf residues and messes of fine organic matter; Js, horizon containing small amounts of organic matter but never biomacrostructured; A, horizon with mixed organic and mineral material with generally a pedological structure of biological origin; M, friable or soft, unbroken or broken rock horizon; ca, presence of carbonates (denomination after [1]). H1 to H3 are situated in the willow plots colonized by vegetation for about 20 years, while H4 to H6 are located in the alder plots colonized for 25–30 years.

H5; oligomull for H4; and dysmull for H6. Two types of calcareous organo-mineral horizons located just under the soil surface were observed (J_{sca} and A_{ca}). The A horizons were biomacrostructured while the Js horizons were “young”, weakly differentiated and containing small amounts of organic matter [1].

The M horizons were sandy for each site, but fine sand was observed for the M horizon of site H4 and for the IIM horizon of H5 and H6. The thickness of these different mineral horizons was almost the same for the six sites.

3.2. Enchytraeid and earthworm communities

Despite no significant differences, the abundance of enchytraeids (Fig. 3) tended to be twice lower in H2 compared to other sites. With regard to earthworm diversity (Table 2), 11 different species were recorded: *Lumbricus castaneus*, *Lumbricus terrestris*, *Lumbricus rubellus*, *Dendrobaena octaedra*, *Dendrobaena pygmaea*,

Dendrobaena rubida, *Aporrectodea rosea*, *Nicodrilus caliginosus caliginosus*, *Nicodrilus nocturnus*, *Octolasion cyaneum*, *Octolasion tyrtaeum lacteum*. Earthworms from H2, H4, H5 and H6 were almost exclusively epigeic

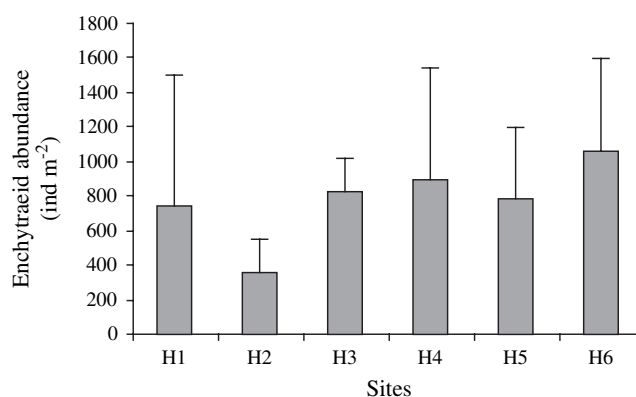


Fig. 3. Mean abundance of Enchytraeids (ind m⁻²) in the different sites H1 to H6. Bars indicate the standard deviations.

Table 2

Ecological categories (Ecol. cat.; epi, epigeic forms; ane, anecic forms; endo, endogeic forms; juv., juveniles), numbers (no m⁻², %), biomass (g m⁻², %) and ratio biomass (Ratio; g ind⁻¹) of earthworms in the six sites H1 to H6

Sites	Species	Ecol. cat.	Numbers, no m ⁻²	% of total number	Biomass, g m ⁻²	% of total biomass	Ratio, g ind ⁻¹
H1	<i>Dendrobaena octaedra</i>	epi	50.67	28	3.37	7	0.07
	<i>Lumbricus rubellus</i>	epi	1.33	1	0.43	1	0.32
	<i>Dendrobaena rubida</i>	epi	2.67	1	0.15	0.5	0.06
	Epigeic sp. juv.	epi	9.33	5	2.10	4.5	0.23
	<i>Lumbricus terrestris</i>	ane	2.67	1	13.16	28	4.93
	<i>Nicodrilus nocturnus</i>	ane	12.67	7	20.24	4	1.60
	<i>Nicodrilus</i> ssp. juv.	ane	19.33	11	5.90	12.5	0.31
	<i>Octolasion tyrteaum lacteum</i>	endo	21.33	12	6.18	13	0.29
	<i>Nicodrilus caliginosus caliginosus</i>	endo	8.00	4.5	3.11	10	0.39
	<i>Aporrectodea rosea</i>	endo	12.67	7	3.42	7	0.27
	<i>Octolasion cyaneum</i>	endo	13.33	7	4.03	8.5	0.30
	Endogeic sp. juv.	endo	28.00	15.5	1.92	4	0.07
	Total ± S.D.			182.00 ± 42	100	64.01 ± 41.97	100
H2	<i>Lumbricus castaneus</i>	epi	6.67	11	0.78	12	0.12
	<i>D. octaedra</i>	epi	4.00	6.5	0.41	6	0.10
	Epigeic sp. juv.	epi	45.33	74	2.08	31	0.05
	<i>Lumbricus</i> ssp. juv.	ane	1.33	2	0.67	10	0.50
	<i>O. t. lacteum</i>	endo	4.00	6.5	2.69	41	0.67
	Total ± S.D.			61.33 ± 14	100	6.63 ± 3.74	100
H3	<i>D. octaedra</i>	epi	22.00	11	2.17	1	0.10
	<i>L. rubellus</i>	epi	10.67	6	7.57	8	0.71
	Epigeic sp. juv.	epi	30.67	16	1.94	2	0.06
	<i>L. terrestris</i>	ane	10.00	5	34.64	36	3.46
	<i>Lumbricus</i> ssp. juv.	ane	2.97	2	3.48	4	1.17
	<i>O. t. lacteum</i>	endo	88.00	46	34.86	36	0.40
	<i>N. caliginosus caliginosus</i>	endo	17.33	9	9.38	10	0.54
	<i>A. rosea</i>	endo	4.67	2	1.90	2	0.41
	Endogeic sp. juv.	endo	5.33	3	0.86	1	0.16
	Total ± S.D.			191.64 ± 80	100	96.8 ± 65.87	100
H4	<i>D. octaedra</i>	epi	8.67	4	0.63	2	0.07
	<i>L. rubellus</i>	epi	2.67	1.5	2.07	7	0.78
	<i>D. pygmea</i>	epi	4.00	2	0.05	0.5	0.01
	<i>D. rubida</i>	epi	24.00	12	1.26	4	0.05
	Epigeic sp. juv.	epi	91.33	45	4.02	14	0.04
	<i>O. t. lacteum</i>	endo	40.00	20	15.61	53	0.39
	<i>N. c. caliginosus</i>	endo	1.33	0.5	0.41	1.5	0.31
	<i>A. rosea</i>	endo	8.00	4	3.29	11	0.41
	Endogeic sp. juv.	endo	22.67	11	1.95	7	0.09
	Total ± S.D.			202.67 ± 71	100	29.29 ± 3.51	100
H5	<i>D. octaedra</i>	epi	3.33	10.5	0.25	6	0.08
	<i>D. pygmea</i>	epi	1.33	4	0.02	0.5	0.02
	Epigeic sp. juv.	epi	7.33	23	0.33	7.5	0.05
	<i>O. t. lacteum</i>	endo	6.67	21	2.74	65	0.41
	Endogeic sp. juv.	endo	13.33	41.5	0.88	21	0.07
	Total ± S.D.			31.99 ± 14	100	4.22 ± 2.31	100
H6	<i>D. octaedra</i>	epi	10.67	8.5	1.07	7.5	0.10
	<i>L. rubellus</i>	epi	1.33	1	0.99	7	0.74
	<i>D. rubida</i>	epi	6.67	5	0.72	5	0.11
	Epigeic sp. juv.	epi	95.33	74.5	3.97	27.5	0.04
	<i>O. t. lacteum</i>	endo	12.67	10	7.52	52	0.59
	Endogeic sp. juv.	endo	1.33	1	0.11	1	0.08
	Total ± S.D.			128.00 ± 32	100	14.38 ± 6.35	

S.D., standard deviation.

and/or endogeic and contained a lot of juveniles (Fig. 4). Anecic species were recorded in H1 and H3, *L. terrestris* in both sites while *N. nocturnus* was only found in H1. Earthworm abundance (Table 2) was higher in H1, H3 and H4 (182.0, 191.6 and 202.7 individuals m^{-2} ,

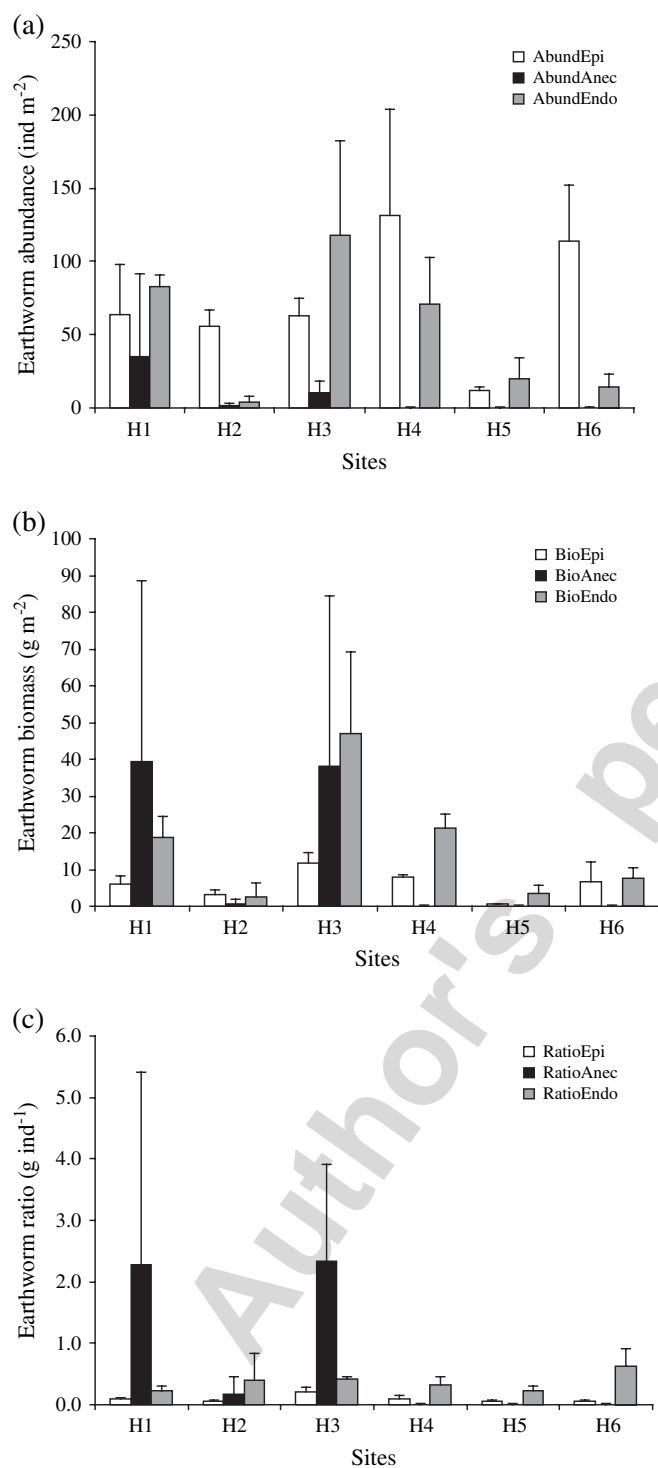


Fig. 4. Mean (a) abundance of epigeic earthworms (ind m^{-2}), (b) biomass (g m^{-2}) and (c) earthworm ratio (g ind^{-1}) in the studied sites H1 to H6 (standard deviation in bars).

respectively) compared to H5 and H2 (32.0 and 61.3 individuals m^{-2} , respectively). Epigeic species were highest in H4 and H6 while endogeic species were more present in H3 and H1. Regarding the identified species, *O. t. lacteum* was dominant in H3 and H4 and *D. octaedra* in H3. However, it should be noted that the proportion of unidentified epigeic species was very high in H2 and H6 (74%), H4 (45%) and H5 (23%), as well as the proportion of unidentified endogeic species in H5 (41.5%). In terms of biomass (Table 2), the global mean values were lowest in H2 and H5 (6.6 and 4.2 g m^{-2} , respectively) while it was largest in H3 (96.8 g m^{-2}). The endogeic and anecic biomasses were the highest in H3, followed by H1, but a high standard deviation was observed. Looking at the ratio biomass giving the mean weight of all individuals in each site, it appears clearly that the largest worms were located in H3 (0.51 g ind^{-1}), the smallest in H2, H4, H5 and H6 (0.11, 0.14, 0.13 and 0.11 g ind^{-1} , respectively), and that an intermediate ratio was found in H1 (0.35 g ind^{-1}). The same tendency was observed when ecological categories were studied separately but with a high standard deviation. Not only the number of worms but also the individual biomass contributed to the relative percentage of the total biomass.

No significant correlation was found between abundance and biomass of each ecological category on the one hand and other biotic or abiotic parameters on the other hand.

3.3. Soil analysis

The six organo-mineral horizons A_{ca} and/or J_{sca} differed in the physicochemical values especially with regard to the particle size distribution (Table 3). Despite a different tree cover and a different location within the transect, the J_{sca} horizons of H2 and H6 were enriched in coarse sand (74.7% and 51.8%, respectively). In contrast, H3 contained the highest proportion of clay (23.1%) and almost no coarse sand (7.4%). H1, H4 and H5 had medium values of each particle size (Table 3). The M horizons were particularly rich in coarse sand but poor in clay and silt compared to the upper layers. Thus, the nature (texture, carbonate content) and the thickness of these underlying deposits were similar for the six sites. The mean weight diameter (MWD) of soil aggregates was negatively correlated with the coarse sand content ($r = -0.96$, 95%, $P < 0.01$) while an opposite tendency was observed for both fine silt and clay contents ($r = 0.94$ and 0.95 , respectively, 95%, $P < 0.01$).

The amount of total carbonate was higher in willow plots H2 (67%), H1 (56.4%), H3 (44.6%) than in other sites (around 35%). In addition, the relatively high

Table 3
Physicochemical characteristics in the different horizons (see Fig. 2) from the six sites H1 to H6

Sites	Horizons	pH	Total CaCO ₃ (%)	Active CaCO ₃ (%)	Fe _t (g kg ⁻¹)	S.D. Fe _o (g kg ⁻¹)	S.D. Fe _d (g kg ⁻¹)	Fe _d - Fe _o /Fe _t ratio	Fe _o /Fe _d ratio	C _{org} (%)	N _{tot} (%)	C/N	Coarse sand (%)	Fine sand (%)	Coarse silt (%)	Fine silt (%)	Clay (%)	MWD (mm)	S.D.			
H1	J _{sca}	7.9	56.4	20.0	14.8	0.12	1.4	0.009	4.1	0.02	18.2	34.1	2.8	0.2	14	33.2	20.9	12	18.9	15	0.908	0.023
	M _{ca}	8.6	66.2	13.8	—	—	—	—	—	—	0.6	0.04	—	72.4	15.6	3.7	5.7	2.6	—	—		
H2	J _{sca}	8.1	67.0	10.9	10.1	0.05	0.5	0.0002	2.2	0.001	16.8	22.7	1.2	0.1	12	74.7	5.9	4.6	9.9	4.9	0.389	0.004
	M _{ca}	8.3	72.4	7.5	—	—	—	—	—	—	0.2	0.03	—	93.7	3.5	0.9	2.0	0	—	—		
H3	A _{ca}	7.9	44.6	20.8	19.7	0.04	2.2	0.002	6.5	0.02	21.8	33.8	3.5	0.2	17	7.4	21.7	17.2	30.6	23.1	1.168	0.031
	M _{ca}	8.5	76.1	10.4	—	—	—	—	—	—	0.4	0.3	—	84.1	9.5	1.8	4.3	0.2	—	—		
H4	A _{ca}	7.9	35.0	18.0	22.6	0.07	2.5	0.014	5.7	0.015	14.2	43.9	2.9	0.2	13	20.6	32.2	18.8	17.2	11.2	0.868	0.037
	M _{ca}	8.3	39.4	16.2	—	—	—	—	—	—	1.2	0.08	—	35.5	35.8	12.8	11.4	4.6	—	—		
H5	A _{ca}	7.8	35.0	19.4	21.7	0.14	2.3	0.017	5.7	0.02	15.7	40.3	5.4	0.4	15	20.7	27	12.8	22.1	17.3	1.039	0.007
	M _{ca}	8.5	54.5	8.9	—	—	—	—	—	—	0.8	0.05	—	76.8	12.3	2.6	6.8	1.5	—	—		
	IIM _{ca}	8.3	43.5	18.1	—	—	—	—	—	—	1.5	0.1	—	42.1	25.2	11.3	12.9	8.5	—	—		
H6	J _{sca}	7.4	33.9	10.5	18.3	0.04	2.0	0.007	4.8	0.03	15.3	41.7	12.1	0.9	13	51.8	9.7	10.3	15.5	12.7	0.733	0.007
	M _{ca}	8.1	56.5	10.1	—	—	—	—	—	—	—	—	1.5	0.1	—	63.9	17.9	5.0	8.8	4.4	—	—
	IIM _{ca}	8.2	43.9	15.0	—	—	—	—	—	—	—	—	1.1	0.08	—	37.0	40.3	9.1	9.8	3.7	—	—

pH, total and active carbonates (Total CaCO₃ and Active CaCO₃, in %), iron forms (Fe_o: amorphous iron; Fe_d: crystallized iron; Fe_t: total iron, in g kg⁻¹), iron form ratios (Fe_d - Fe_o/Fe_t, Fe_o/Fe_d), organic carbon (C_{org}, in %), total nitrogen (N_{tot}, in %) and C/N ratio, soil texture (coarse and fine sand, coarse and fine silt, clay, in %), mean weight diameter (MWD, in mm). Iron forms were only measured on organo-mineral horizons and the C/N ratio and MWD were only calculated for J_{sca} and/or A_{ca} horizons. Standard deviations (S.D.) are given for iron forms and MWD.

content of active carbonate (20%) found in H1, H3, H4 and H5 was negatively correlated with the coarse sand content ($r = -0.89$, 95%, $P < 0.05$). The organic matter showed great variations along the transect, with high contents in H6 (12.06% and 0.91% for C_{org} and N_{tot} , respectively). However, the C/N ratios remained quite constant except for H5 (15.2) compared to a value of around 13–14 for the other sites.

As for iron forms, concentrations of total iron Fe_t were highest in the alder community sites H4 (22.6 g kg⁻¹) and H5 (21.7 g kg⁻¹) compared for instance to H2 (10.1 g kg⁻¹). These values were inversely proportional to coarse sand content. A significant positive correlation was found between Fe_t , Fe_o , Fe_d and the coarse silt content (respectively $r = 0.85$, $r = 0.87$, $r = 0.89$, 95%, $P < 0.05$), but no other significant correlation was found with another mineral fraction. The values of Fe_d were low for H2 (2.2 g kg⁻¹) and high for H3 (6.5 g kg⁻¹) and showed a positive correlation with the MWD ($r = 0.91$, 95%, $P < 0.05$). The same tendency could be observed for the values of Fe_o

(low for H2 and H1; 0.5 and 1.4 g kg⁻¹, respectively). But these two iron forms showed a significant negative correlation with the coarse sand amount ($r = -0.92$, 95%, $P < 0.01$ for Fe_d ; $r = -0.82$, 95%, $P < 0.05$ for Fe_o). The ratio Fe_o/Fe_d increased gradually from H2 (22.7) to H5 (40.4) with a peak in H4 (43.9) and a negative correlation was observed between Fe_o/Fe_d and the total carbonate content ($r = -0.94$, 95%, $P < 0.01$).

As a complement to biological variables, the $Fe_d - Fe_o/Fe_t$ ratio, which represents an index of the soil evolution and increases with time, was positively related to the biomass of anecic earthworms ($r = 0.85$, 95%, $P < 0.05$) while the abundance of enchytraeids was negatively related to the total carbonate amount ($r = -0.88$, 95%, $P < 0.05$).

3.4. PCA synthesis

The principal component analysis (PCA, Fig. 5) illustrates in a two-way axis the relationships between all measured variables. The first principal component

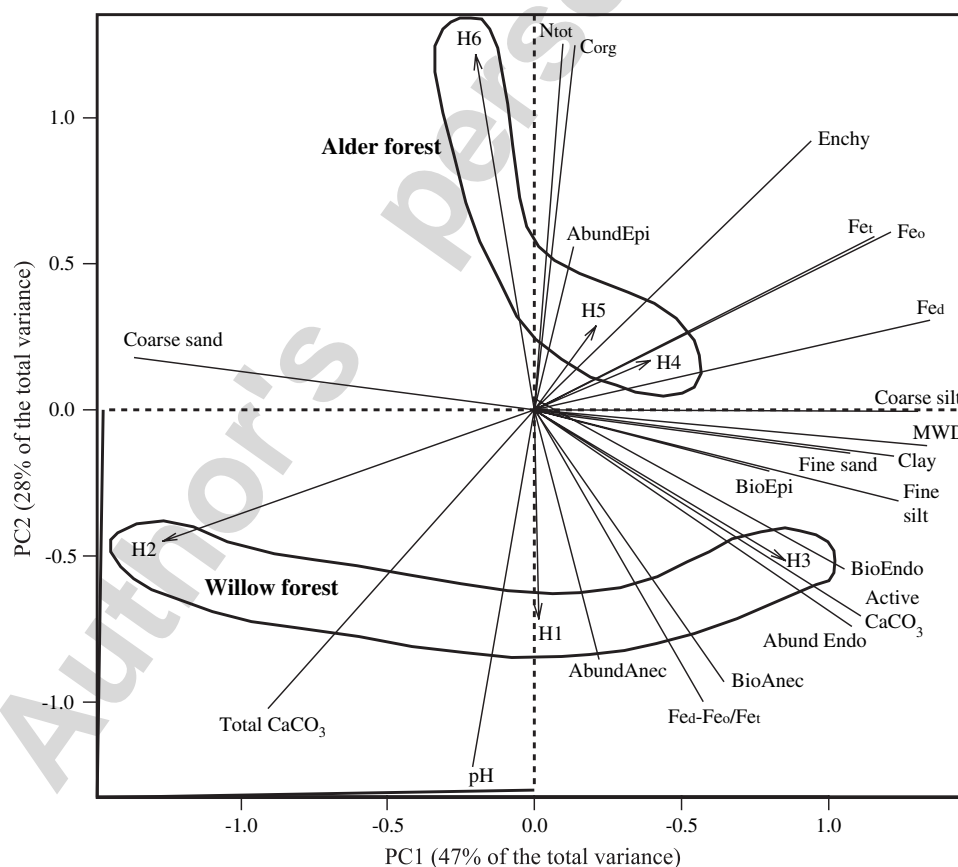


Fig. 5. Results of the principal component analysis (PCA): ordination of the samples (H1 to H3: willow plots; H4 to H6: alder plots) and the variables in the plane defined by the axis PC1 and PC2. Variables: codes as in Table 3; Enchy, enchytraeid abundance; AbundEpi, epigeic earthworm abundance; BioEpi, epigeic earthworm biomass; AbundAnec, anecic earthworm abundance; BioAnec, Anecic earthworm biomass; AbundEndo, endogeic earthworm abundance; BioEndo, endogeic earthworm biomass.

axis PC1 (explaining 47% of the total variance) separated the samples according to the particle size distribution (except the coarse sand), the MWD and the biomass of epigeic and endogeic earthworms on the right side. The second axis PC2 (explaining 28% of the total variance) discriminated the forest types with alder plots at the top and willow plots at the bottom. Along this same axis, differences were also visible between pH values (at the bottom) and contents of C_{org} and N_{tot} (on the top).

The PCA showed a relationship between most of the biological parameters (biomass and abundance of worms) and the sites H3, as well as H1 to a lesser extent. However, no strong relations appeared between earthworm's criteria and the different iron forms, except for $Fe_d - Fe_o/Fe_t$ ratio that was more related to anecic earthworms.

Furthermore, the site H2 was clearly correlated with the coarse sand and the carbonates, while H4 and H5 were more related to the number of enchytraeids, the abundance of epigeic earthworms and the different iron forms. These iron forms were also more associated with the coarse silt content than other particle size parameters and were closed to the MWD. No strong relations appeared between the soil texture and the concentrations of C_{org} and N_{tot} revealing no evident difference between H3 and the alder plots (H4, H5 and H6).

4. Discussion

4.1. Biological parameters

Enchytraeids are an important group of the soil mesofauna in most temperate terrestrial biotopes [37]. The density of enchytraeids is generally higher in acid soils with important organic content [13]. Thus, the high pH values found in our soils could explain the low average abundance of enchytraeids compared to the values reported for an intensively cultivated agricultural soil, dry sclerophyll forests or a peat moor [13,17]. The slightly greater abundance in H6 could be due to the highest content of organic carbon found in that site. As enchytraeid densities are usually associated with soil moisture and silty particles, their low abundance in our case may also be due to the unfavourable conditions of humidity due to the particle size distribution (sandy soils are drier than silty soils). Another reason for this low abundance could be the competition with earthworms, since they have been often reported to have a considerable effect on enchytraeid populations: in an acid (pH 4.5) deciduous forest [43], they were shown to drastically decrease their abundance, while

other authors also suggested a negative relationship between enchytraeids and earthworms at different acidities (pH 4.9 and pH 6.1 in unlimed or limed forest soil respectively) [44]. Moreover, an antagonistic relationship was also found in a polder soil, which showed less enchytraeids upon inoculation with earthworms [17]. Nevertheless, this last author also demonstrated that both groups showed optimal population development at different temperatures and moisture levels, suggesting that in natural environments, they occupy different ecological niches.

Another reason for the relatively low abundance of enchytraeids could be the sampling period. Samples were collected during summer time and high temperatures may have killed or forced a part of the population to move to the deeper soil layers. Due to a variable abundance of enchytraeids (see the high standard deviations), no statistical difference between the six soils was found. But as soil structure actors, and even if the abundance is low, enchytraeids affect soil structure by producing faecal pellets that influence aggregate stability by creating favourable habitats for microorganisms [13]. These microorganisms are also known to have a great influence on the decomposition of freshly fallen leaf litter [56] and form micro-aggregates after soil organic matter consumption. Particles aggregation is then stimulated, which greatly improves the soil structure [28]. This influence is particularly relevant in initial stages of soil structure formation, as investigated here, where earthworm communities are still not well developed.

In the present study, abundance and biomass of earthworms were similar to those recorded in a subtropical forest in Athens (GA, USA) with sandy loam to sandy clay loam soils [10] or in various woodland types on clay or limestone soils [14]. A study of earthworm distribution within different humus forms in beech forests [51] gave a mean abundance of 220 individuals m^{-2} and a mean biomass of 116 $g m^{-2}$ for a rich mull humus form. These data are comparable to our site H3 and to H1 and H4 for the mean abundance. However, our results were much higher than those of Zorn et al. [57], who observed only five different species in an active floodplain system. This low diversity was explained by the climatic conditions in the Netherlands with long periods of flooding. Our study site could then not be considered as an active floodplain system but, in contrast, as a stable dynamic alluvial system. The relative contribution of juveniles to the average abundance and biomass of our studied plots is quite similar to studies conducted in a deciduous forest in the United States [50] where juveniles accounted for

approximately half of the total biomass and of the total number of individuals.

Concerning the epigeic category, the preponderance of *D. octaedra* in H1, H3, H4 and H6 indicated a higher degree of organic matter humification than in other plots [50]. The other epigeic species *L. rubellus*, indicating less humified conditions, was also present in H1, H3, H4 and H6, but to a lesser extent. This species plays a major role in the first steps of aggregation because it adds numerous secretions to soil as it passes through the gut and thus increases the organic carbon content in casts [48]. The absence of this species in H2, associated with a sandy texture difficult to ingest and to stabilize in aggregates could explain the lower aggregate stability reflected by the low MWD. In addition, *L. castaneus*, which indicates a reduced organic matter content, dominated in H2. In contrast, the presence of *D. pygmaea* in H4 is a sign of high content of organic matter and possibly a sign of sand as well [7]. The high number of *D. rubidus* in H4—and in H6 to a lesser extent—indicated a good biological activity in the upper layers. This species is known to be ubiquitous and very mobile in the superficial layers of soil and has been reported to consume a proportionately greater amount of organic matter than deeper-burrowing species [29].

The anecic category was only present in H1 and H3. The deep-burrowing *L. terrestris* was dominant in H3 and represented one third of the total biomass. This species is known to have a positive effect on soil structure by creating mixing casts of organic and mineral particles. These casts may then be hardened into stable soil aggregates and provide a food source for other animals in deeper soil strata [46]. The massive abundance and biomass of *L. terrestris* in H3 and the smallest abundance in H1 can be explained by the soil texture. According to Cuendet [14], this species prefers a soil formed of limestone layer instead of clay, and Curry [15] demonstrated a positive relationship between clay content and different species including *L. terrestris*. Thus, a sandy texture is not favourable for worms because the low water content does not maintain the hydrostatic pressure and then does not prevent desiccation [57]. In abrasive gravelly soils the earthworm skin could be injured because of its softness [13,15]. This constraint is particularly true for the anecic category (but also for the endogeic one), which contributes also to the mixing of organic and inorganic material in deep layers (bioturbation). Thus, the soil texture can explain the absence of anecic earthworm in H4, H5 and H6 despite the oldest age of tree population, compared with the three other sites.

The endogeic category was mostly present in H1, H3 and H4 with the dominance of *O. t. lacteum*. This neutrophilous species plays a major role in the stabilization of organic matter by incorporating litter fragments into the mineral layers. This bioturbation is a key process in the formation of mull humus forms [19] and the presence of anecic and endogeic earthworms in soils, as observed for H1, H3 and H4, has a critical impact on soil structure, aggregate formation and stability.

Thus, the present paper suggests that, in terms of soil biota succession, epigeic earthworms are probably the first engineers, with enchytraeids, in the initial steps of soil structuring. Then, if the soil texture is favourable, the anecic and endogeic earthworms rapidly invade the different soil layers and improve the physical and nutrient conditions.

4.2. Physicochemical characteristics

In this study the effect of the particle size distribution of the surface horizons on soil structure was evident. As the nature and thickness of the underlying mineral horizons (alluvium gravel and M horizons) were similar, we could then exclude in our case their influence on structure of the upper horizons. Thus, aggregate stability, illustrated by MWD, is strongly dependent on the particle size distribution of the recent deposits and not only on the duration of soil evolution. We did not find, in contrast to many authors [20,42,53], a positive correlation between organic carbon content and aggregation. In our case, the aggregate stability was positively correlated with enchytraeid abundance, coarse and fine silt, and clay content of A and/or J horizons, as well as with different iron forms and negatively correlated with coarse sand content. The “young” site H3 showed the highest MWD value with fine sand, fine silt and clay contents. It is well recognized that clay particles are particularly involved in the soil structure with an increase of aggregate stability when clay content increases [30]. But it has until now never been demonstrated that the fine parts of sand particles as well as the silt particles also participate to aggregate stability. Boix-Fayos et al. [6] showed that large aggregates (>5 mm) were positively correlated with the amount of sand but this occurred in the presence of earthworms producing casts. It has already been shown that medium-textured soils appear to be more favourable to earthworms than sandy soils or soils with high clay content [15]. Shipitalo and Protz [48] also showed that sand content was significantly lower and the clay content greater in casts of small worms such as *L. rubellus*

than in casts of the large worm *L. terrestris*. In our case, the site H3 presented these expected conditions and was indeed rapidly colonized by anecic earthworms that produced stable aggregates in spite of a recent and silty sand deposit.

Data for iron forms found in this work were quite similar to other studies [25] or a little lower [3]. Our data showed that among the “youngest” (in terms of sediment deposition and age of present tree population) sites H1, H2 and H3, the stability of aggregates increased with the increase of various iron forms proportions. These iron forms and particularly the Fe_o type are usually considered as cement particles in water-stable aggregates [20] and are related here to the fine particles of soil. It is known that clay and Fe_d contents are significantly and positively correlated in the upper layers [25,35], but it was revealed by our correlation analysis that the coarse silt fraction was the prime supplier of Fe_t . In addition, Fe_d , which increases with increasing soil formation age, was also associated to the silt particles in our alluvial context. Clearly, fewer proportions of various iron forms were extracted from the coarse sandy H2, implying a reduced aggregate stability.

Calcium carbonates are also known to act as cementing agents by maintaining the flocculated structure or the clay in soil-surface aggregates through acid neutralization [21]. In our study, this content was not correlated to any textural classes and calcium carbonates were distributed equally among the different textural fractions. But the negative correlation with Fe_t and Fe_o forms revealed that the carbonated part of soil was characterized by a weak iron content. Moreover, the active calcium carbonates, which represent the finest fraction of total calcium carbonate and binding particles, showed a low calcium availability in the coarse sand fraction. In our study, this coarse sand fraction played clearly a major role in the aggregate stability and influenced strongly the humus form evolution.

5. Conclusions

The study of soil biological and physicochemical processes on initial stages of soil structure formation in two different tree population types brought new observations to light:

1. The distribution of earthworm categories depends on the soil texture of the recent deposits and not only on the soil age that is reflected by the colonizing age of tree populations. Soil biota succession

appears in two steps: epigeic earthworms with enchytraeids are the first engineers producing in a short-term soil structure and then, if texture is favourable, anecic and endogeic earthworms invade the different soil layers improving physical and nutrient conditions and creating long-term stable aggregates.

2. The particle size distribution of the upper horizon strongly influences aggregate stability that is weak in the presence of coarse sand content and stronger with fine silt and clay contents. When the structure stability increases, a positive feedback appears and accelerates the formation of large aggregates despite a recent and silty sand deposit. No strong influence of the underlying mineral horizons (alluvial gravel or buried mineral horizon) was found.
3. Iron forms acting as cementing agents in soil aggregation are observed in the coarse silt fraction representing the prime supplier of iron and are found in low amounts in the coarse sand fraction.
4. Calcium carbonates are equally distributed among the different textural fractions. However, the negative correlation between active calcium carbonate fraction, representing the finest part of total calcium carbonate, and the coarse sand content could also explain a lack of aggregate stability in this textural class. Active calcium carbonate seems to be a good agent for binding organic matter with mineral components.

In conclusion, we showed in our study that the tree population age cannot be used alone as an indicator of the humus form formation and evolution. Biological and physicochemical parameters, especially particle size distribution and earthworm categories, also strongly influence aggregation in the initial phases of soil structure formation in an alluvial context, such as the Sarine River. These differences in soil development induce a heterogeneous distribution of the humus forms that increases the ecological value of the alluvial zone and the continuity of ecosystem functions.

Acknowledgements

The authors are grateful to Dr Fabrice Bureau for scientific and technical support and Dr Thibaud Decaens for identification of different earthworm species. We also acknowledge Dr Florian Kohler for his statistical analysis assistance and Dr Laure Weisskopf for her constructive comments on the manuscript. Additional

thanks are extended to anonymous reviewers for valuable comments on revising the manuscript.

References

- [1] AFES (Association Française pour l'Etude du Sol), A sound reference base for soils, the "référentiel pédologique", Edition INRA, 1998.
- [2] D.A. Angers, G.R. Mehuys, Aggregate Stability to Water, in: M.R. Carter (Ed.), Soil Sampling and Methods of Analysis, Canadian Society of Soil Science, 1993, pp. 651–662.
- [3] E. Arduino, E. Barberis, F. Carraro, M.G. Forno, Estimating relative ages from iron-oxide/total-iron ratios of soils in the western Po Valley, Italy, *Geoderma* 33 (1984) 39–52.
- [4] E. Arduino, E. Barberis, F. Ajmone Marsan, E. Zanini, M. Franchini, Iron oxides and clay minerals within profiles as indicators of soil age in northern Italy, *Geoderma* 37 (1986) 45–55.
- [5] R. Bauer, C. Kampichler, A. Bruckner, E. Kandeler, Enchytraeids (Oligochaeta) in an Austrian spruce forest: abundance, biomass, vertical distribution and re-immigration into defaunated mesocosms, *Eur. J. Soil Biol.* 30 (1994) 143–148.
- [6] C. Boix-Fayos, A. Calvo-Cases, A.C. Imeson, M.D. Soriano-Soto, Influence of soil properties on the aggregation of some Mediterranean soils and the use of aggregate size and stability as land degradation indicators, *Catena* 44 (2001) 47–67.
- [7] Bouché, M.B. Lombriciens de France. Ecologie et systématique, Editions INRA, 1972.
- [8] M.B. Bouché, R.H. Gardner, Earthworm functions, VIII. Population estimation techniques, *Rev. Ecol. Biol. Sol.* 21 (1984) 37–63.
- [9] G. Bullinger-Weber, J.-M. Gobat, Identification of facies models in alluvial soil formation: the case of a Swiss alpine floodplain, *Geomorphology* 74 (2006) 181–195.
- [10] M.A. Callahan, P.F. Hendrix, Relative abundance and seasonal activity of earthworms (Lumbricidae and Megascolecidae) as determined by hand-sorting and formalin extraction in forest soils on the southern Appalachian Piedmont, *Soil Biol. Biochem.* 29 (1997) 317–321.
- [11] L.H. Cammeraat, A.C. Imeson, Deriving indicators of soil degradation from soil aggregation studies in southeastern Spain and southern France, *Geomorphology* 23 (1998) 307–321.
- [12] C. Chenu, Y. Le Bissonnais, D. Arrouays, Organic matter influence on clay wettability and soil aggregate stability, *Soil Sci. Soc. Am. J.* 64 (2000) 1479–1486.
- [13] D.C. Coleman, D.A. Crossley, P.F. Hendrix, *Fundamentals of Soil Ecology*, Elsevier Academic Press, 2004.
- [14] G. Cuendet, A comparative study of the earthworm population of four different woodland types in Wytham woods, Oxford, *Pedobiologia* 26 (1984) 421–439.
- [15] J.P. Curry, Factors affecting the abundance of earthworms in soils, in: C.A. Edwards (Ed.), *Earthworm Ecology*, 2nd edition, CRC Press, Boca Raton, 2004, pp. 91–113.
- [16] W. Didden, H. Born, H. Domm, U. Graefe, M. Heck, J. Kühle, A. Mellin, J. Römbke, The relative efficiency of wet funnel techniques for the extraction of Enchytraeidae, *Pedobiologia* 39 (1995) 52–57.
- [17] W. Didden, H.-C. Fründ, U. Graefe, Enchytraeids, in: G. Benckiser (Ed.), *Fauna in Soil Ecosystems*, Marcel Dekker, 1997, pp. 135–172.
- [18] A.K. Dolui, R. Bera, Relation between iron forms and pedogenic processes in some alfisols of Orissa, India, *Agrochimica* 45 (2001) 161–170.
- [19] C.A. Edwards, P.J. Bohlen, *Biology and Ecology of Earthworms*, Chapman and Hall, 1996.
- [20] E.T. Elliott, Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils, *Soil Sci. Soc. Am. J.* 50 (1986) 627–633.
- [21] W.W. Emerson, D.J. Greenland, Soil aggregates—formation and stability, in: M.F. De Boodt, M.H.B. Hayes, A. Herbillon (Eds.), *Soil Colloids and Their Associations in Aggregates*, Plenum Press, New York, 1990, pp. 485–511.
- [22] M.H. Garvin, F. Martinez, J.B. Jesus, M. Gutierrez, P. Ruiz, D.J. Diaz Cosin, Effect of *Hormogaster elisae* (Oligochaeta; Hormogastridae) on the stability of soil aggregates, *Eur. J. Soil Biol.* 37 (2001) 273–276.
- [23] C. Guenet, F. Bureau, G. Weber, F. Toutain, Initial stages of soil formation in a riparian zone: importance of biological agents and lithogenic inheritance in the development of the soil structure, *Eur. J. Soil Biol.* 35 (1999) 153–161.
- [24] R. Ihaka, R. Gentleman, R: a language for data analysis and graphics, *Journal of Computational and Graphical Statistics* 5 (1996) 299–314.
- [25] M. Kahle, M. Kleber, R. Jahn, Carbon storage in loess derived surface soils from Central Germany: influence of mineral phase variables, *J. Plant Nutr. Soil Sci.* 165 (2002) 141–149.
- [26] Kemper, W.D., Rosenau, R.C. Aggregate stability and size distribution, in: A. Klute (Ed.), *Methods of Soil Analysis, Part 1*, 2nd edition, Agron. Monogr. 9, ASA and SSSA, Madison, WI, 1986, pp. 425–442.
- [27] K. Klinka, Q. Wang, R.E. Carter, Relationships among humus forms, forest floor nutrient properties, and understory vegetation, *Forest Sci.* 38 (1990) 564–581.
- [28] L.S. Koutika, W.A.M. Didden, J.C.Y. Marinissen, Soil organic matter distribution as influenced by enchytraeid and earthworm activity, *Biol. Fertil. Soils* 33 (2001) 294–300.
- [29] C.J. Langdon, T.G. Pearce, A.A. Meharg, K.T. Semple, Survival and behaviour of the earthworms *Lumbricus rubellus* and *Dendrodrilus rubidus* from arsenate-contaminated and non-contaminated sites, *Soil Biol. Biochem.* 33 (2001) 1239–1244.
- [30] Y. Le Bissonnais, Aggregate stability and assessment of soil crustability and erodibility: I. Theory and methodology, *Eur. J. Soil Sci.* 47 (1996) 425–437.
- [31] J.C.Y. Marinissen, F. van den Bosch, Colonization of new habitats by earthworms, *Oecologia* 91 (1992) 371–376.
- [32] J.C.Y. Marinissen, W.A.M. Didden, Influence of the Enchytraeid worm *Buchholzia appendiculata* on aggregate formation and organic matter decomposition, *Soil Biol. Biochem.* 29 (1997) 387–390.
- [33] J.C.Y. Marinissen, E. Nijhuis, N. van Breemen, Clay dispersability in moist earthworm casts of different soils, *Appl. Soil Ecol.* 4 (1996) 83–92.
- [34] O.P. Mehra, M.L. Jackson, Iron oxide removal from soils and clays by a dithionite citrate system buffered with sodium bicarbonate, *Clays Clay Miner.* 7 (1960) 317–327.
- [35] J.M. Oades, Associations of colloids in soil aggregates, in: M.F. De Boodt, M.H.B. Hayes, A. Herbillon (Eds.), *Soil Colloids and their Associations in Aggregates*, Plenum Press, New York, 1990, pp. 463–483.
- [36] J.M. Oades, The role of biology in the formation, stabilization and degradation of soil structure, *Geoderma* 56 (1993) 377–400.

- [37] F.B. O'Connor, The Enchytraeidae, in: A. Burges (Ed.), Soil Biology, Academic Press, London and New York, 1967, pp. 213–257.
- [38] M. Pansu, J. Gautheyrou, L'analyse du sol minéralogique, organique et minérale, Springer, Paris, 2003.
- [39] N. Patzel, J.-F. Ponge, The heterogeneity of humus components in a virgin beech forest, Eur. J. Soil Biol. 37 (2001) 117–124.
- [40] G.E. Petts, C. Amoros, Fluvial Hydrosystems, Chapman and Hall, London, 1996.
- [41] J.-F. Ponge, Humus forms in terrestrial ecosystems: a framework to biodiversity, Soil Biol. Biochem. 35 (2003) 935–945.
- [42] P. Puget, C. Chenu, J. Balesdent, Total and young organic matter distributions in aggregates of silty cultivated soils, Eur. J. Soil Biol. 33 (1995) 449–459.
- [43] M. Rätty, Growth of *Lumbricus terrestris* and *Aporrectodea caliginosa* in an acid forest soil, and their effects on enchytraeid populations and soil properties, Pedobiologia 48 (2004) 321–328.
- [44] M. Rätty, V. Huhta, Earthworms and pH affect communities of nematodes and enchytraeids in forest soil, Biol. Fertil. Soils 38 (2003) 52–58.
- [45] J. Rouiller, Analyses des sols, techniques de laboratoire, Centre de pédologie biologique, CNRS, Nancy, Note technique no. 32, 1981.
- [46] M. Schaefer, J. Schauer mann, The soil fauna of beech forests: comparison between a mull and a moder soil, Pedobiologia 34 (1990) 299–314.
- [47] S. Schrader, M. Langmaack, K. Helming, Impact of collembola and enchytraeidae on soil surface roughness and properties, Biol. Fertil. Soils 25 (1997) 396–400.
- [48] M.J. Shipitalo, R. Protz, Factors influencing the dispersibility of clay in worm casts, Soil Sci. Soc. Am. J. 52 (1988) 764–769.
- [49] M.J. Shipitalo, R.C. Le Bayon, Quantifying the effects of earthworms on soil aggregation and porosity, in: C.A. Edwards (Ed.), Earthworm Ecology, 2nd edition, CRC Press, Boca Raton, 2004, pp. 183–200.
- [50] R.M. Snider, R.J. Snider, ELF ecological monitoring in Michigan. II. The earthworm communities of test and control sites, Pedobiologia 32 (1988) 335–342.
- [51] H. Staaf, Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types, Oecologia 72 (1987) 58–64.
- [52] U. Schwertmann, Differenzierung der Eisenoxide des Bodens durch Extraktion mit Ammoniumoxalat-Lösung, Z. Pflanzenernähr. Düng. Bodenkd. 105 (1964) 194–202.
- [53] J.M. Tisdall, J.M. Oades, Organic matter and water-stable aggregates in soils, J. Soil Sci. 33 (1982) 141–163.
- [54] X31-105, Calcaire total, évaluation des carbonates, in: AFNOR (Eds.), Qualité des sols méthodes d'analyse, Association Française de Normalisation, 1987, pp. 37–40.
- [55] P.C.J. van Vliet, D.C. Coleman, P.F. Hendrix, Population dynamics of Enchytraeidae (Oligochaeta) in different agricultural systems, Biol. Fertil. Soils 25 (1997) 123–129.
- [56] V. Wolters, Effects of *Mesenchytraeus glandulosus* (Oligochaeta, Enchytraeidae) on decomposition processes, Pedobiologia 32 (1988) 387–398.
- [57] M.I. Zorn, C.A.M. Van Gestel, H. Eijsackers, Species-specific earthworm population responses in relation to flooding dynamics in a Dutch floodplain soil, Pedobiologia 49 (2005) 189–198.