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Earthworm activity and soil structure changes due to organic enrichments in vineyard systems

Received: 4 August 1997

Abstract The effect of organic enrichment on earthworm activity and soil structure was studied in two French vineyards, by comparing control and test plots. In each vineyard the organic matter quantitatively increased the abundance and biomass of the earthworm community. These increases were associated with a higher level of species diversity and a higher evenness corresponding to the development of endogeic community. These earthworm community changes were associated with an increase in granular bioturbated areas and in macroporosity in the top soil layer. The micromorphological approach incorporated an original process of image analysis which appeared to be an appropriate method for characterizing pore morphology in this study. The pores when characterized by their size and shape could be related to ecological groups and growth stages of earthworms.

Key words Organic matter · Earthworm activity · Soil structure · Micromorphology · Image analysis

Introduction

Soil is considered as an interactive system in which the different compartments are strongly interrelated, in particular: soil structure, flora and fauna, and organic matter (Coleman and Odum 1992). The earthworms act on soil structure by: (1) ingestion of soil, partial breakdown of organic matter, intimate mixing of these fractions, and ejection of this material as surface or sub-

surface casts and (2) the formation of excavations such as burrows (Jacot 1936; Edwards and Lofty 1977; Rogaar and Boswinkel 1978; Satchell 1983; Lee 1985; Curry 1987). Moreover, their dynamics and behaviour are influenced by the trophic richness of soils (Raw 1962; Bostrom 1987; Cluzeau et al. 1990; Binet 1993).

Study on this interactive system (Gillot-Villeneuve 1994) has shown how important it is to consider the earthworm population in terms of functional composition species composition instead of their global abundance and biomass only. These results have been reinforced with some descriptive studies of soil structures associated with earthworm activities (Kretzschmar 1982, 1987, 1990; Shaw and Pawluck 1986; McKenzie and Dexter 1993; Elton and Koppi 1994). However, Lopes-Assad (1987) showed that the identification of earthworm species was not sufficient on its own to relate structural morphology to in situ biological activity of species. It was also necessary to consider the growth stage of the earthworm.

Thus, this in situ study had two aims. The first was to assess the influence of organic matter on earthworm activities and assess the two main structural modifications which resulted: (1) structural modifications associated with casts, (2) biopores. The second was to relate the morphological features of the biological pores to the activity of particular earthworm species. To this end, earthworms were characterized by their species and their growth stage, and pores were characterized by their size and shape. This morphological approach was carried out using an original process of image analysis.

The study was conducted in two French vineyards: in the Champagne and Burgundy regions. In these agrosystems which presented strong anthropogenic constraints, organic matter was supplied for fertilization and to limit erosion.

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Material and methods

Study sites

The field experiment was carried out in two French vineyards: (1) in Champagne (Montbré site), where the soil was a sandy-loam clay and the vineyard had been replanted in 1988; (2) in Burgundy (Mâcon site), where the soil was a loamy clay and the vineyard had been planted in 1986 after maize and corn farming. Since planting, no tillage or superficial mechanical practices were applied. At each site, a control plot was compared to a test plot which had received two organic enrichments during the last 4 years: fresh poplar bark (Montbré) and resinous bark compost (Mâcon).

Earthworm community

The earthworms were sampled by the formaldehyde method (Bouché 1969), with three replications at each plot. The earthworm community was characterized by its abundance (no. m⁻²), biomass (g m⁻²), species and ecological structure (Lee 1959; Bouché 1972; Table 1) and age ratio. The earthworm community was subdivided into four functional groups: A, B, C, D (Table 2), in order to relate fauna activity to soil structure. These functional groups were based on the following characteristics: growth stage, ecological category and diameter of adults (Bouché 1972). In our study, all *Allolobophora chlorotica chlorotica typica* individuals were less than 5 mm in diameter, and therefore adults were considered as belonging to group C.

Soil structure

Samples

The top 24 cm of soil, where biological activity is most important, was studied. For each plot, three undisturbed soil blocks (8 cm high × 15 cm wide × 5 cm thick) were sampled. They corresponded to three study zones: L1 (0–8 cm), L2 (8–16 cm) and L3 (16–24 cm). In the laboratory, the blocks were treated with a water/acetone exchange in the liquid phase and were impregnated with a polyester resin (Crystic) containing a UV fluorescent dye (Uvitex; Murphy et al. 1977). From each block, a large thin section (16 cm × 9 cm) was made.

Qualitative description of structural changes

Thin sections were observed with the naked eye and by optical microscopy to describe the soil structure. Two main structural components, one dense and one porous, were apparent. The mor-

Table 2 Earthworm functional group (A, B, C, D) and individual diameter in each functional group according to growth stage and ecological category

Growth stage	Ecological category	
	Epigeic + Endogeic	Anecic
Juveniles	A (0–2 mm)	B (0–5 mm)
Adults	C (2–5 mm)	D (5–9 mm)

phological characteristics of the latter (aggregate size and shape) were similar to those related to earthworm casts (Pawluck 1987; Fitzpatrick 1993). The extent of each of the structural components was quantified and the ratio between the cast and the total thin section area was called the “bioturbated area ratio”.

Quantitative description of biological macropores

Image analysis was used to characterize biological macropores, which were considered to be the result of earthworm activity only, according to field observations. Image capture and treatment were performed on a Sun Sparc IPC Station, with a Sony CCD camera using Noesis Visilog software. For each thin section, three windows (52.5 mm × 37.8 mm) were digitized in a rectangular grid of 768 × 576 pixels, with a spectral resolution of 256 grey levels and a spatial resolution of 70 µm per pixel. Each window provided two images corresponding to the capture under two light conditions: reflected UV light, and reflected visible light. Under UV light, the fluorescent dye included in the resin showed up bright on a dark background; thresholding the grey-level image gave a binary image displaying bright areas, which corresponded to both the macropores and to microporous calcareous concretions. Under visible light, calcareous concretions showed up bright on a dark background; thresholding the image gave a binary image which corresponded to the calcareous concretions only. By subtraction these two binary images gave an image corresponding to the macropores only. This image was filtered to remove pores with cross sectional area less than 0.4 mm² (80 pixels).

In order to distinguish between biological macropores and other macropores (cracks, voughs), it was necessary to locate them on each image and to separate them from other macropores. This operation was performed manually by comparing the image with the sample. It enabled the elimination of artefacts, taking into account the casts within the channels, and identification of macropores with a double origin (mechanical and biological), which are common problems when using tomography (Joschko et al. 1993).

Table 1 Diameters of adults of each species observed (Bouché 1972), and presence (+) or absence (–) at both experimental sites

Ecological group	Species	Adult diameter	Montbré	Mâcon
Epigeic	<i>Lumbricus castaneus</i> (Savigny 1826)	2–2.5	+	+
	<i>Eisenia eiseni</i> (Levinsen 1884)	2–3	+	–
	<i>E. fetida</i> (Savigny 1826)	2–4	+	–
Anécic	<i>Aporrectodea longa</i> (Ude 1886)	5.5–8	+	+
	<i>Aporrectodea giardi</i> (Savigny 1826)	5–7	+	+
	<i>L. terrestris</i> (Linnaeus 1758)	7–9	+	+
Endogeic	<i>Allolobophora chlorotica chl. typica</i> (Savigny 1826)	3–7	+	+
	<i>Allolobophora rosea rosea</i> (Savigny 1826)	2–3.5	+	+
	<i>Aporrectodea caliginosa</i> (Savigny 1826)	3.5–4.5	+	+
	<i>Allolobophora icterica</i> (Savigny 1826)	3–4	+	+

		pore shape classes (elongation index)						
		S1 (<1)	S2 (1-2)	S3 (2-3)	S4 (3-4)	S5 (4-5)	S6 (5-7)	S7 (>7)
s	A1 (<1)							
	A2 [1-2]	I		II				III
	A3 [2-3]							
m	A4 [3-4]		IV			V		VI
	A5 [4-5]							
l	A6 [5-6]		VII		VIII			IX
	A7 [6-7]							X

Fig. 1 Pores size classes (A) according to equivalent diameter and pore shape classes (S) according to elongated index. 4 size classes: *s* small; *m* medium; *l* large; *vl* very large; 3 shapes: ▨ rounded; ▩ intermediate; □ elongated. 10 morphological classes: I-X; (-) do not exist

Each biological macropore was then characterized by two morphological parameters: (1) its size, *A*, estimated by the surface area (mm^2) of its section on the image, (the ratio between the total area of these sections and the total surface of the image gave the “surfacing porosity”) (2) its shape, *S*, estimated by the elongation index defined by Coster and Chermant (1989) as

$$S = \text{perimeter}^2 / 4\pi \text{ area}$$

$S=1$ for a rounded pore, and the higher *S*, the more elongated is the pore. This index allowed distinction between rounded shapes (corresponding to normal sections of a channel), intermediate shapes (corresponding to pores with an irregular perimeter) and elongated shapes (corresponding to tangential sections). These two parameters are complementary, as shown by Kretzschmar (1982): the origin of a channel cannot be determined by its size only.

In order to relate pore morphology to earthworm species, biological macropores were classified according to several size and shape classes (Fig. 1): (1) seven size classes (A1–A7) were recognized according to the equivalent diameter of the pore and to the diameter of adult earthworms (Bouché 1972) and their observed biodiversity (Table 1); (2) seven shape classes (S1–S7) were defined by arbitrarily dividing the whole range of *S* values. In some studies (Hallaire and Cointepas 1993; Binet et al. 1997), these two parameters could be taken into account separately for a morphological characterization of pore space. By contrast, in this study, it appeared that they should be analyzed together, because the elongation index did not correspond to the same shape according to pore size: for example the shape class, S6, corresponded to an elongated shape for size class A2 (1–2 mm equivalent diameter) and to an intermediate shape for size class A6 (5–6 mm equivalent diameter). This led us to combine pore and shape parameters according to the observed functional groups. This combination allowed us to reduce the number of classes from seven to four for size (*s*, small; *m*, medium; *l*, large; *vl*, very large) and from seven to three for shape (*r*, rounded; *i*, intermediate; *e*, elongated). Figure 1 shows the relationship between these classes and the *S* and *A* classes; this combination defines ten morphological classes (I–X).

Results

Earthworm community

Observed earthworm abundances (Fig. 2) were similar to results obtained in other studies under the same conditions (Cluzeau et al. 1990). The global abundance was

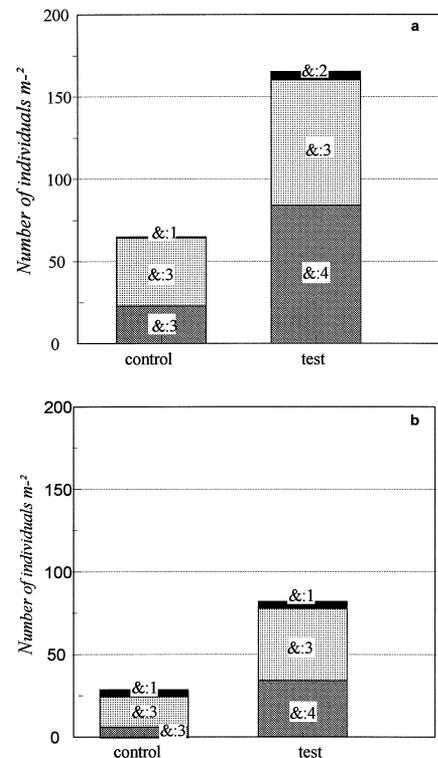


Fig. 2 Abundance of earthworms at Montbré (a) and Mâcon (b). Ecological category: ■ epigeic; ▨ anecic; ▩ endogenic. &:1-4 indicates the number of species recorded

significantly higher in the Montbré site (65–165 individuals m^{-2}) than in the Mâcon site (27–78 individuals m^{-2}) (Mann-Whitney, threshold 0.05%). The first site seemed to present better general characteristics (type of organic enrichment, texture, history, agricultural practices) for earthworm development. In both sites, organic matter enrichment was associated with a significant increase in the abundance and the biomass of the community (Mann-Whitney, threshold 0.05%). At both sites, all the communities included three anecic species and three or four endogenic species (Fig. 2). Without organic matter enrichment, anecics significantly dominated (Mann-Whitney, threshold 0.05%) the community (63%), but with organic enrichment, endogenic development was stimulated (Mâcon, 53%; Montbré, 46%). Changes in the proportions of the functional groups were related to the increase in the number of taxa: development of *A. icterica* at both sites and of *Eisenia eiseni* at Montbré. In terms of species composition, organic matter seemed to be beneficial, particularly for *A. chlorotica chlorotica typica* and to a lesser extent for *A. rosea rosea*. At both sites, the communities were dominated significantly (Mann-Whitney, threshold 0.05%) by juveniles (67–76%), the lowest rate being observed for the area without organic matter amendment at Mâcon (Fig. 3). At both sites in the control plots without organic matter, the juvenile communities as well as the adult communities were significantly (Mann-Whitney, threshold 0.05%) dominated by

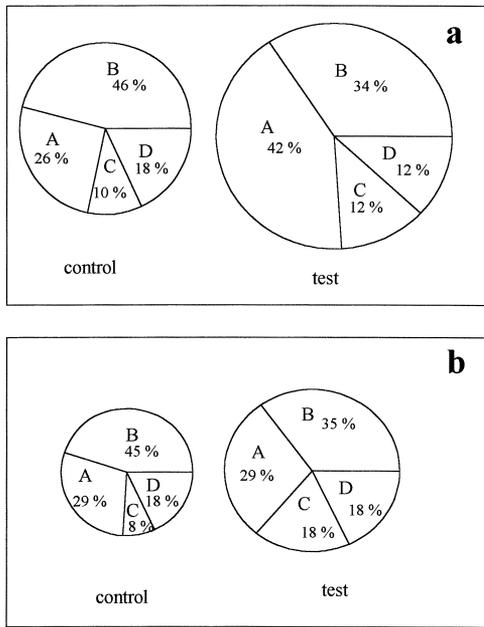


Fig. 3 Age ratio of functional groups at Montbré (a) and Mâcon (b). A Juveniles (epigeic and endogeic); B anecic juveniles; C adults (epigeic and endogeic); D anecic adults

anecics, whereas in the test plots with organic matter, the juvenile communities were either significantly (Mann-Whitney, threshold 0.05%) dominated by endogeics (Montbré) or the evenness was higher, due to the increase in the number of endogeic individuals (Mâcon), and the evenness of the adult communities was higher.

Soil structure

Qualitative description of structural modifications

At Montbré (sandy loam clay texture), the bioturbated area ratio for the whole area of the thin section (Fig. 4)

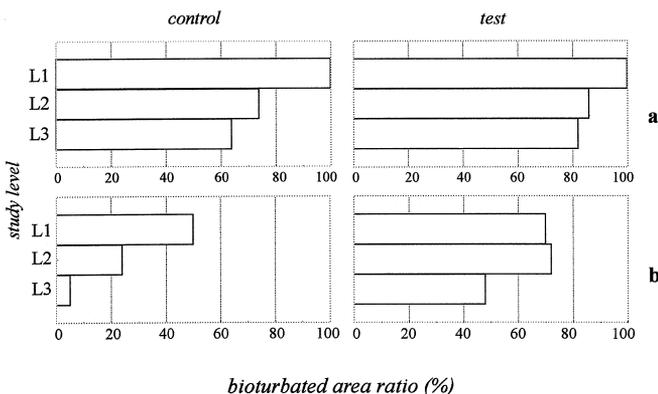


Fig. 4 Bioturbated area ratio in relation to the study level in control and test plots at Montbré (a) and Mâcon (b). L1 0–8 cm depth, L2 8–6 cm depth, L3 16–24 cm depth

was 80% in the control plot and 90% in the test plot. These results were higher than those for Mâcon (loamy clay texture) where the ratio was 28% in the control plot and 63% in the test plot. This ratio was influenced by the type of soil, thus these results complemented the observations made by Shaw and Pawluck (1986), but the ratio was also influenced by earthworm activity. In major plots (test and control plots at Montbré and test plot at Mâcon), the bioturbated area ratio was highest in level L1.

At Montbré, the bioturbated area ratio in the control was too high to assess any influence of organic enrichment. At Mâcon, the bioturbated area ratio in the test plot (with organic enrichment) was more than 155% that of the control plot (corresponding to 50–70% of the thin-section area).

Quantitative description of the biological macropores

The surfacic porosity of the samples classified according to pore shape and size is shown in Fig. 5. Pore numbers are given in Table 3.

At Montbré, organic enrichment was associated with an increase in the surfacic porosity and in the number of pores. In the control plot, the porosity was qualitatively and quantitatively variable over the whole profile: (1) the surfacic porosity increased from L1 to L2, then decreased to L3; (2) the pore number decreased from L1 (165) to L2 (145), and to L3 (103). The pore space in L1 consisted of a high number of essentially rounded small and medium pores. It consisted of larger pores in L2. In the test plot with organic enrichment, the surfacic porosity and pore number changed in the same way over the whole profile. L1 was characterized by an association of medium and large pores, and elongated ones, while L2 and L3 were dominated by medium pores, with rounded and intermediate shapes.

At Mâcon, organic enrichment caused an increase in the total surfacic porosity and in the total pore number. In the control plot the surfacic porosity showed little variation throughout the whole profile; there was a slight increase in the pore number from L1 (117) to L2 (128), then a decrease to L3 (89). Pore space comprised mainly small and medium pores with rounded and intermediate shapes. In the test plot with organic enrichment, the surfacic porosity showed little variation throughout the whole profile; the pore number increased from L1 (119) to L2 (155) and to L3 (179). Very large, elongated burrows were present in level L1 and progressively disappeared with depth, whereas rounded pores with different sizes (small to large) became more and more numerous.

Fig. 5 Surfacing porosity at Montbré (a) and Mâcon (b) classed on size and shape of the pores. *s* Small; *m* medium; *l* Large; *vl* very large;  rounded;  intermediate;  elongated. *px:y* Indicates total surfacing porosity (y) for each soil zone (x)

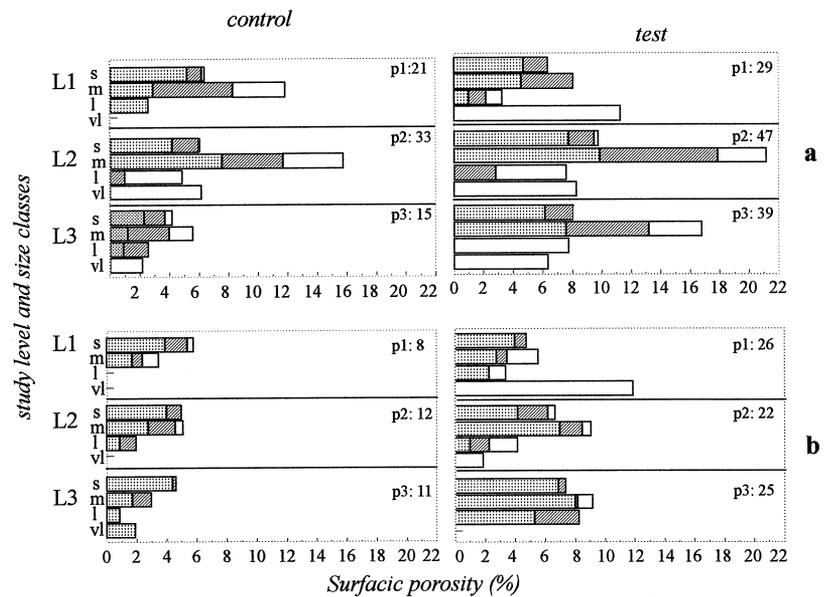


Table 3 Numbers of pores for each soil zone studied (*L1* 0–8 cm, *L2* 8–16 cm, *L3* 16–24 cm) according to pore size (*s* small, *m* medium, *l* large, *vl* very large) and pore shape (*r* round, *i* intermediated, *e* elongated) at both experimental sites

Soil zone	Pore shape	Pore number according to pore size															
		Montbré								Mâcon							
		Control				Test				Control				Test			
	<i>s</i>	<i>m</i>	<i>l</i>	<i>vl</i>	<i>s</i>	<i>m</i>	<i>l</i>	<i>vl</i>	<i>s</i>	<i>m</i>	<i>l</i>	<i>vl</i>	<i>s</i>	<i>m</i>	<i>l</i>	<i>vl</i>	
L1	<i>r</i>	109	12	0	0	97	20	1	0	61	9	0	0	78	9	2	0
	<i>i</i>	24	14	0	0	31	11	1	0	35	3	0	0	19	2	0	0
	<i>e</i>	2	9	1	0	0	0	1	3	5	4	0	0	0	6	1	2
L2	<i>r</i>	60	27	0	0	155	36	0	0	87	12	1	0	84	20	1	0
	<i>i</i>	26	12	0	0	32	23	2	0	19	6	1	0	38	5	1	0
	<i>e</i>	1	12	3	3	5	8	4	3	1	1	0	0	1	2	2	1
L3	<i>r</i>	53	5	0	0	140	26	0	0	73	4	0	0	136	28	4	0
	<i>i</i>	26	6	0	0	32	15	0	0	7	3	0	0	7	1	2	0
	<i>e</i>	6	4	0	1	1	7	6	2	0	0	1	1	0	1	0	0

Discussion

Earthworm abundance and soil structure related to organic enrichment

To characterize the interactive system, surfacing porosity and bioturbated area ratio were related to earthworm abundance (Fig. 6). Montbré presented a higher earthworm abundance than Mâcon and the bioturbated area ratio and surfacing porosity were also significantly higher at Montbré. The physical and chemical characteristics of each site and their agricultural practices influenced the macrobiological abundance and consequently the soil structure itself.

The individual burrowing activity of earthworms was higher in the controls at both sites (Table 4). This result reflected the earthworms' search for food, which is

more important without organic matter enrichment, as has been observed in many laboratory studies (Evans 1947; Jefferson 1956; Jeanson 1968; Martin 1982; Elton and Koppi 1994). However, in our field study, organic enrichment at both sites increased earthworm abundance and consequently the surfacing porosity. This observation showed the advantage of stimulating earthworm community dynamics in order to improve soil

Table 4 Individual burrowing activity of earthworms according to organic enrichment

	Surfacing porosity per earthworm (%)	
	Montbré	Mâcon
Control	35	37
Test	23	31

macroporosity. This enrichment was also profitable in that it conferred a higher stability to the aggregates and, in turn, to the granular structure (Guckert 1967; Jeanson 1968). This could explain observations made on the Mâcon control where, in spite of the low number of earthworms (27 individuals m^{-2}), the pore number was high, indicating high macrobiological activity, but the bioturbated area ratio remained low (5–50%).

Pore morphological characteristics related to earthworm species' activity

The relationship between pore morphology and earthworm activity (Table 5) was based on a combination of data corresponding to the age ratio of the functional group (Fig. 3), pore number (Table 3) and knowledge of burrow morphology and earthworm behaviour. Anecic species are known to live in permanent burrows that are open at the surface (Lee and Foster 1991) and their casts are usually on the surface, while endogeic species make extensive burrows that ramify through the soil but are rarely open to the surface, are less permanent than those of anecic species, and some of their sections are frequently filled with casts (Lee and Foster 1991).

We distinguished between two types of pores: (1) those resulting from recent earthworm activities and which could be related to the earthworm population observed, and (2) those resulting from former earthworm activities.

At both sites, pore space in the whole profile included a high number of small, rounded pores (72–82% of total pores). According to the earthworm community structure (dominated by juveniles: 64–76%), these could be associated with the recent activities of anecic, endogeic or epigeic juveniles. Small pores with an intermediate shape, corresponding to burrows filled with casts or obliterated burrows, could be related to the former activity of anecic individuals or to recent endogeic activity. Small elongated pores could not be associated with the activity of any particular species.

At both sites, medium pores (rounded and intermediate shapes) were more prevalent in L2 and L3 in the plots with organic enrichment, whereas in the control plots this type of pore was more prevalent in L1 and L2. The presence or absence of trophic resources ap-

parently have some influence on the behaviour of the earthworms responsible for this type of pore: with organic enrichment these earthworms were mainly located in the lower layers, while without organic enrichment they were more active in the top layers. Presumably, this type of behaviour could be associated with endogeic earthworms, as was shown by Jeanson (1968). Thus, medium rounded pores could be associated with recent activities of endogeic adults (or epigeic adults, but the former were thought to more abundant in view of the earthworm population composition and earthworm localisation in the profile), and also with recent activities of juvenile anecics, especially for pores located in the top layers (Lee and Foster 1991; Kobel-Lamparski and Lamparski 1987). Medium pores with an intermediate shape corresponded to sections of burrows filled by casts and were either related to recent activities of endogeic adults (casual burrows) or to former activities of adults of no particular ecological group. Medium pores with an elongated shape could not be associated with the activity of any particular earthworm species.

The number of large pores, particularly those with a rounded or intermediate shape, was very low in both sites (1–2%; except in Mâcon with organic enrichment). Because of their size, they were related to the activities of anecic adults which comprised 12–18% of the total populations. The low number of pores could be explained by the permanent burrowing habit of anecics (Lee and Foster 1991). Moreover, the vertical orientation of burrows created by anecics (Lee and Foster 1991; Kretzschmar 1982) are not readily observed in vertical sections. Thus, the large pores with rounded shape could be related to recent activities of anecic adults, while those with intermediate shape could correspond to sections through crowded burrows which were no longer used and were related to former activities of anecic adults. Elongated large pores, which were more abundant than the other pore shapes, correspond to longitudinal sections of burrows. They could be related to recent activities of adults, especially endogeic ones: endogeics create horizontal burrows, in the form of an extensive network (Lee and Foster 1991).

The number of very large pores was very low (0.3–1.2% of the total); they were always elongated and could be associated with recent activities of adult anecics, their distribution throughout the whole profile characterizing the drilling activity typical of anecic species.

We noticed that even though the number of large and very large pores was very low at both sites, these pore types, in test plots, represented 50% of the surfacic porosity; most of them were associated with the activities of anecics, demonstrating the dominant influence of anecics on the dynamics of soils.

In conclusion, our study, carried out in situ, yielded results that were in accordance with well known relationships between organic matter, earthworm activity and soil structure, but the particular interest of this

Table 5 Relationship between morphological pore characteristics (*size, shape*) and earthworm functional group (*A, B, C, D*). For abbreviations, see Table 2

Size	Shape		
	r	i	e
s	A, B	A, C	?
m	B, C	C	?
l	D	D	C, D

study was its qualitative approach to examining this interactive system:

1. Organic matter increased the abundance and biomass of the earthworm communities, but also our study showed that at both sites these increases were associated with a higher level of species diversity and a higher evenness (how equally abundant the species are, *sensu* Margurran 1983) corresponding to the development of the endogeic community, particularly to the development of *Allolobophora chlorotica chlorotica typica*.

2. The influence of this increase on the soil was characterized by the improvement in the quality of soil porosity, i.e. an increase in the bioturbated area (porous structure) and an increase in the surfacic porosity.

In order to relate soil structure to earthworm activity, instead of trying to relate earthworm burrows defined by their size, length or orientation to an aspect of earthworm activity (Kretzschmar 1982, 1990; Lopes-Asad 1987), we attempted to associate morphological characteristics of biological pores with the activities of earthworm species. To achieve this, biological pores were characterized by their size and shape, two parameters which seemed to be pertinent to our approach to the problem. These parameters were derived from image analysis, a method which appeared appropriate for characterizing the morphology of biological macropores. Even if it was not possible for us to associate a specific pore morphology with the activity of a particular earthworm species, our study shows that it is possible to associate a type of pore, characterized by its size and shape, with a particular group of earthworms characterized by their ecological category and growth stage. To facilitate a species-based approach, these results indicate the need for: (1) monospecific studies in the laboratory to create a data base relating observed biostructure to each earthworm species and growth stage; (2) a better characterization of pore morphology taking into account their orientation.

To overcome the difficulty of recording vertical burrows, more sections per sampled soil block appear necessary. Furthermore, the study of pores in two dimensions, achieved by image analysis, could be complemented by observation of soil blocks in three dimensions, using X-ray computed tomography.

Acknowledgements Yannick Bénard, Unite de Sciences du Sol, INRA Rennes, is gratefully acknowledged for his technical assistance. This work was supported by the Comité Interprofessionnel des Vins de Champagnes within the project "Vignes et Vins Septentrionaux".

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