

F. Bastardie · M. Cannavacciuolo · Y. Capowiez
J.-R. de Dreuzy · A. Bellido · D. Cluzeau

A new simulation for modelling the topology of earthworm burrow systems and their effects on macropore flow in experimental soils

Received: 15 March 2002 / Accepted: 12 June 2002 / Published online: 13 August 2002
© Springer-Verlag 2002

Abstract Earthworm burrows (i.e. macropores) are organised in burrow systems with various geometric properties. These burrow systems have a significant effect on soil processes, particularly the movement of water in the soil. But the relationships between earthworm burrow systems and their hydraulic properties are not well established because experimental studies of burrow geometry are difficult to perform. Although X-ray computed tomography has revolutionised the 3D description of burrow systems, this method is both time consuming and expensive. This paper presents a new, cheap and rapid approach. A computer model simulating the burrowing behaviour of earthworms was developed from experimental studies. A saturated flow model was then superimposed on the structure of the simulated burrow system to explore the relationships between the burrow systems and their hydraulic properties. Simulations of individual burrow systems were obtained for two different species of earthworm belonging to different ecological groups. Structural parameters of burrow systems (pore space, interconnectedness, connectivity and the number of openings at the limits of the space) were calculated and linked with estimates of permeability using regressions. In our results connectivity gave the best prediction of the difference in permeability between the two sets of burrow systems determined by the burrowing behaviour of the earthworms. Pore space, interconnectedness and the number of burrow openings explained fewer variations.

Keywords Earthworm · Burrow systems · Simulation model · Topology · Behaviour

Introduction

Many authors have demonstrated that burrows play a key role in water infiltration, nutrient transfer and gas diffusion (Elhers 1975; Beven and Germann 1982; Edwards et al. 1990; Bouma 1991). However, few authors had access to burrows in real burrow systems because until recently the description of their 3D characteristics was difficult. Most of the studies were based on a 2D slice of soil and attempted to correlate the number of pores, pore diameter and vertical pore distribution at different depths in the soil profile using infiltration measurements (Stockdill 1982; Smetten and Collis-Georges 1985; Zachmann et al. 1987; Ela et al. 1992; Knight et al. 1992; Urbanek and Dolezal 1992; Munyankusi et al. 1994; Piktanen and Nuutinen 1995; Francis and Fraser 1998). Some of these works produced contradictory results probably because the 3D organisation of burrow systems was not taken into account. As a matter of fact, continuity and connectivity are essential factors in water transfer and it is necessary to understand both the topology of the burrow systems and its variability (McCoy et al. 1994). As postulated by Smetten (1992), knowledge of this architecture may enable better prediction of their hydraulic properties.

Moreover, studies based on 2D slices and infiltration measurements did not pay attention to the observed macroporosity is the result of burrowing by several species with different activities. Three major ecological categories of earthworm can be distinguished by their life history (Bouché 1977; Lee 1985) and burrow systems (Lee and Foster 1991; Jégou et al. 1998):

1. Epigeic species affect surface crusting or could occlude macropores.
2. Endogeic species make sub-horizontal or randomly oriented burrows, which are more or less temporary constructions because they are rarely reused.

F. Bastardie (✉) · M. Cannavacciuolo · A. Bellido · D. Cluzeau
Laboratoire Fonctionnement des Ecosystèmes
et Biologie de la Conservation, UMR CNRS 6553 Ecobio,
Station Biologique, 35380 Paimpont, France
e-mail: francois.bastardie@univ-rennes1.fr

Y. Capowiez
Laboratoire de Toxicologie Environnementale,
UMR 406 Ecologie des invertébrés INRA/UAPV,
84914 Avignon Cedex 09, France

J.-R. de Dreuzy
Géosciences, Campus de Beaulieu – Université de Rennes 1,
263, Avenue du général Leclerc, 35042 Rennes Cedex, France

3. Anecic species live in sub-vertical burrows with varying degrees of branching which are used as “shelters” from where the earthworms come to the soil surface to find their food.

These differences in ecological behaviour result in burrow systems with different geometry.

A non-destructive technique, namely computer-assisted tomography, has revolutionised the description of earthworm burrow systems by permitting their reconstruction in 3D (Joschko et al. 1991; Daniel et al. 1997; Capowiez et al. 1998; Jégou et al. 1998, 1999; Langmaak et al. 1999; Capowiez et al. 2000a, 2000b). It has also allowed the quantification of 3D characteristics such as the continuity of burrows and connectivity between burrows. This kind of analysis together with measurements of infiltration through burrow systems could provide geometrical characteristics to be linked with particular hydraulic properties of soil (Joschko et al. 1992). However, in order to highlight such a relationship, it would first be necessary to analyse a large number of burrow systems with different topologies. This approach would be expensive and time-consuming using this method.

The simulation of the burrow system and the prediction of infiltration is however a cheap and rapid approach to explore the conceptual relationships between these parameters. It can also simulate earthworm behaviour during the creation of the burrow system, and provide a better characterisation of the water permeability of the burrow systems of each earthworm species, as well as identify the major factors that could cause a difference in water permeability. In the present paper we present and discuss this new approach applied to burrow systems. First, burrow systems were simulated, and then a water flow model was used on each burrow system. This enabled conceptual exploration of the functional importance of their topology on soil hydrology. In contrast with previous studies (Martin and Lavelle 1992; Monestiez and Kretzschmar 1992) we tried to simulate earthworm burrow systems both in a realistic and dynamic way by constructing an animal-oriented model based on earthworm behaviour (moving or burrowing) and the geometry of earthworm burrow systems. Multi-agent simulation (Judson 1994; Ferber 1995) was an appropriate method to take into account variations in the impact of earthworm behaviour on the whole soil process affected by earthworm activity, and in particular on the permeability of burrow systems.

Materials and methods

Simulation input: the behaviour of earthworms

Two specific groups of characteristics of earthworm behaviour were defined for the endogeic species *Allolobophora chlorotica* (Savigny, 1826) and the anecic species *Nicodrilus nocturnus* (Evans, 1946), respectively. These were obtained from the analysis of trajectories of isolated earthworms in a 2D terrarium made by Capowiez (2000) where the successive positions of the earthworms were recorded over 5 days immediately after the worms had been introduced into their new environment. The trajectories of ten adults of each species were reconstructed in this way.

For the purpose of simulation, the continuous movement of earthworms in the soil was split into different types of “movement”. Break points in the earthworm’s trajectory, either reversal of the movement or the beginning of a new burrow, were identified. Six categories of movement (burrowing or moving) were defined: (I) creating a burrow, (II) moving forwards before branching off in a lateral burrow, (III) moving backwards before moving forwards, (IV) moving forwards before moving backwards, (V) moving backwards before branching off in a lateral burrow, (VI) moving forwards before reaching an extremity and digging.

At the end of each movement, the earthworm chooses the following movement. To determine the nature of the following movement, the relative frequencies of these movements were transformed into probabilities of occurrence that were used in the simulation. To determine the length of the following movement, the length of movement was chosen at random in each movement-length distribution (I, II, III, IV and V) that was computed from trajectometry. These lengths of movement were added for all the trajectories of individuals belonging to the same species to the detriment of inter-individual variability.

Simulation input: the geometry of burrow systems

Each burrow was approximated as a series of straight lines called links. Each link has two geometrical characteristics: length and orientation (incline and azimuth in a 3D space). The geometrical characteristics of links used in our simulation were computed after 3D reconstruction of the skeletons of earthworm burrow systems (Capowiez et al. 2000a, 2000b). In this study, eight adult individuals belonging to *A. chlorotica* and four adults belonging to *N. nocturnus* were incubated for 2 months in three microcosms (diameter 16 cm; length 30 cm) of homogeneous soil.

In the present study, these burrow systems were simplified into straight lines (the links) using the following algorithm: successive segments for which the angular deviation between them was inferior to 15° were gathered in a single link. Finally, the length and orientation link distributions (incline and azimuth) of burrow systems were obtained for each microcosm. These distributions were analysed by species to the detriment of inter-individual variability. During the simulation, length and orientation were chosen at random in these distributions. For link orientation, the values were restricted inside the interval between $-\pi/4$ and $\pi/4$ in comparison with the previous link built.

Simulation of earthworm burrow systems: virtual earthworms, links and nodes

A virtual earthworm started from the soil surface and moved in a 3D space represented as a virtual core of homogeneous soil of 40 cm×40 cm×30 cm (Fig. 1). An earthworm that reached the limits of the core was forced to move back even though in experimental soil columns earthworms are used to digging along the PVC wall. In the first step, the simulation was done with one single earthworm in the core.

The virtual earthworms moved different distances depending on the movement-length distributions for type I, II, III, IV or V. In the first version of the model, these movement-length distributions did not vary with depth, the previous movement of the earthworm or time. In reality, these three parameters certainly play a role in earthworm behaviour but we ignored them because data on these effects were too scarce. For each move during the simulation, a length was randomly drawn from previously described distributions, and the earthworm went on burrowing or moving until this distance had been covered. Choice of the following movement was limited by the associated probabilities of occurrence.

The simulated burrow systems (Fig. 1) created by the virtual earthworms were summarised as a set of nodes joined by straight links, i.e. the basic elements of the burrow system. The nature (length and orientation) of the links that made up each new burrow was controlled by the distribution of link characteristics. There are three kinds of nodes, characterised by the number of links around

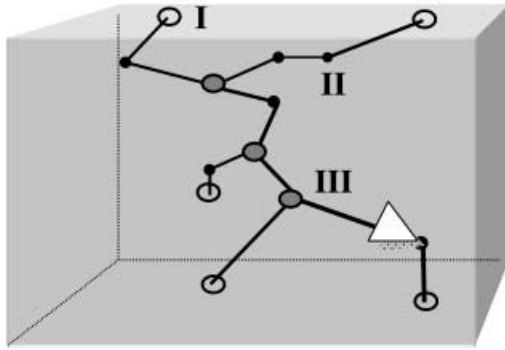


Fig. 1 The virtual earthworm (Δ), the 3D network and the three types of node. I Node extremity (empty circle), II double node (black circle), III triple node (grey circle)

them: (1) a node extremity is a node which has only one link, (2) double nodes are nodes which connect two links, (3) triple nodes connect three links as a result of lateral branching of a new burrow or of an intersection between burrows. The maximal coordination number of the burrow system is three.

During the creation of a burrow by an earthworm, possible intersections with existing burrows were detected and, in this case, the construction was stopped and, in the simulation, the earthworm systematically reused the burrow, although in reality, earthworms behave differently when faced with an existing burrow (Capowiez and Belzunces 2001).

Validation of the simulation of virtual earthworm behaviour

The simulation of the behaviour of virtual earthworms was validated by comparison with input data (trajectometry). Sequences of behaviour, relative frequency, and the distribution of the total distance of movement between the different kinds of moves were computed in 1,000 simulations. These new simulations were realised in an infinite space to eliminate the border effect of simulation. Sequences of behaviour were described by transition probabilities between “burrowing” behaviour (movement type I), “moving forwards” (movement type II or IV) and “moving backwards” (movement type III or V). The percentage of total movement and relative frequency of moves were compared with data from trajectometry by a Kolmogorov-Smirnov test.

Geometrical characterisation of the simulated burrow systems

Simulated burrow systems were characterised by a set of descriptors in order to analyse the geometrical differences in burrow systems between *N. nocturnus* and *A. chlorotica*. The descriptors were: mean link length (a); mean link incline (b); sinuosity of the burrow system which was the deviation between two successive links (c); tortuosity of the burrow system (d), i.e. burrow length divided by the distance between its extremities; rate of branching, i.e. the number of triple nodes divided by total length (e); and rate of burrow extremity (f), i.e. the number of node extremities divided by total length. In previous studies of macroporosity the use of dyes has shown that only a part of burrows or fractures are in fact involved in water flow (Beven and German 1982). Consequently, we computed other descriptors that focused more on the burrow drainage system (i.e. the part of the burrow system where the water flow was not null): the total length of drainage equivalent to the effective macropore space (g); the rate of branching of the burrow drainage system, i.e. the degree of interconnectedness of the effective burrow system, since all links in burrow systems have similar hydraulic properties (constant aperture) (h); the number of nodes at the limits of the space at the surface (i), or at the bottom limit (j); and finally the number of independent paths defined as

the number of paths throughout the core that do not share a link (k). This last parameter is equivalent to the degree of connectivity of the burrow system between the top and the bottom of the core, and it is similar to the “genus” or “cyclomatic number” (Macdonald et al. 1986; Dullien 1992; Spanne et al. 1994). We computed the lengths of these independent pathways. For this last descriptor, we first determined the length of the independent pathway that was the shortest (l ; this length was nearly equivalent to the minimal pathway between the top and bottom of the core). Then, we computed the mean length (m) of the set of independent pathways for each simulated burrow system. Finally, we computed the ratio between the number of paths and the length of this path by using either minimal path length (o) or mean path length (p).

In the first step, the burrow systems were simulated at maximal continuity where movement is possible from any part of the burrow system to any other part. A set of t -tests was realised in order to compare *A. chlorotica* and *N. nocturnus* for each descriptor.

Water flow model

A capillary model of water infiltration (Perrier 1995; de Dreuzy 2000) was used to functionally characterise simulated burrow systems at saturation. This model postulates that the hydric behaviour of the burrow system only depends on the arrangement of a set of simple geometrical shapes. In our case, the latter were perfectly rectilinear cylinders with a constant aperture (i.e. links), which display elementary hydric behaviour based on physical laws. Infiltration was determined at saturation and the soil matrix was considered impermeable, i.e. water diffusion through the burrow lining was neglected. Burrow systems connecting the surface with a depth limit were “infinite clusters” (Robinson 1983) and allowed determination of local flow through them. In contrast, burrow systems that did not reach the bottom of the core had zero permeability and were removed.

The computation of the flow through each link was required to discretise the diffusion equation on the burrow system structure. Each link connecting two nodes was crossed by a flow defined at saturation by Poiseuille’s law:

$$Q_{ij} = K_{ij} \frac{(h_i - h_j)}{L_{ij}} \quad (1)$$

where Q_{ij} is a function of hydraulic charge h_i and h_j at the two extremities, K_{ij} is the hydraulic permeability of each link ($K_{ij}=1$ with constant aperture of links) between nodes i and j and L_{ij} is link length.

Moreover, a flow conservation equation can be written for each node i that has three close neighbours:

$$\sum_{j=1}^{j=3} Q_{ij} = 0 \quad (2)$$

From Eqs. 1 and 2, we obtain for each node i of the burrow system the following equation:

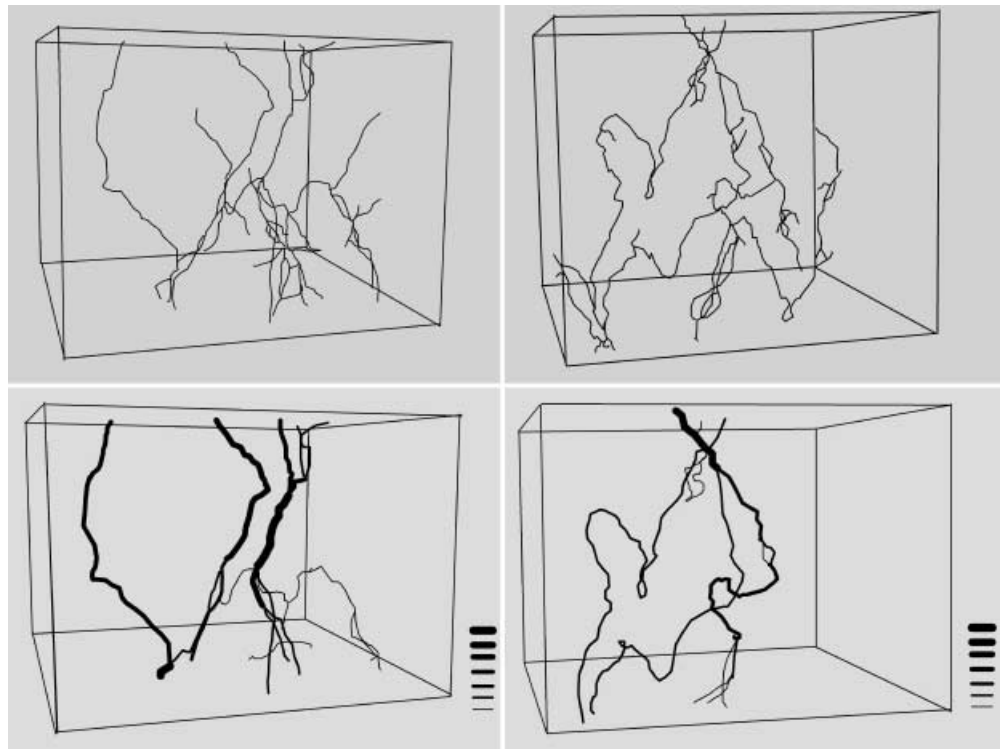
$$\sum_{j=1}^{j=3} \frac{K_{ij}}{L_{ij}} (h_i - h_j) = 0 \quad (3)$$

Taking all the nodes together, the linear system equations obtained can be written under matrix form $Ah=B$ whose dimension equals the number of nodes. Solving this system to find node charges was carried out step by step starting with arbitrarily imposed charges at nodes on the limits of the space until the set of node charges was known. Then the different flows in the burrow system were deduced. The total flow (Q) was the sum of input flows or the sum of output flows. Finally, the total steady-state flow was given by permeability at saturation (K_{sat}) for each simulated burrow system by the equation (for a 3D space):

$$K_{sat} = Q \cdot \frac{H}{S} \quad (4)$$

with S the section of the space simulation and H the difference in hydraulic charge between the top and the bottom of the core. A multiple linear regression was performed in order to link these

Fig. 2 Two examples of simulated burrow systems for the two species *Nicodrilus nocturnus* (left) and *Allolobophora chlorotica* (right). Top Total burrow system, bottom part of burrow systems where flow occurs (the flow increases with an increase in the diameter of the burrows)



permeability values to the total length of drainage with the characteristics of the burrow system topology (number of openings, interconnectedness and connectivity).

Results

Six hundred burrow systems were simulated for the two species *A. chlorotica* and *N. nocturnus*, examples of which are shown in Fig. 2.

Difference in behaviour between *A. chlorotica* and *N. nocturnus*

The percentage of earthworm moves is given in Fig. 3A and Table 1 for the trajectometry and for the simulation, respectively. Experimental data showed that *N. nocturnus* and *A. chlorotica* displayed different behaviour patterns: *A. chlorotica* built more new burrows than it moved inside its existing burrow system (84% of total length for type I against 16% for II, III, IV and V), whereas *N. nocturnus* built less than it moved inside its existing burrow system (21% total length for type I against 79% for II, III, IV and V). Simulation data showed good agreement with the observed data which allows us to affirm that a difference in behaviour exists between the two species: virtual earthworms *A. chlorotica* built 80% of total burrow length and moved in existing burrows only 20% of the total length. In contrast, virtual *N. nocturnus* built 31% of total burrow length and moved in existing burrows 69% of the total length.

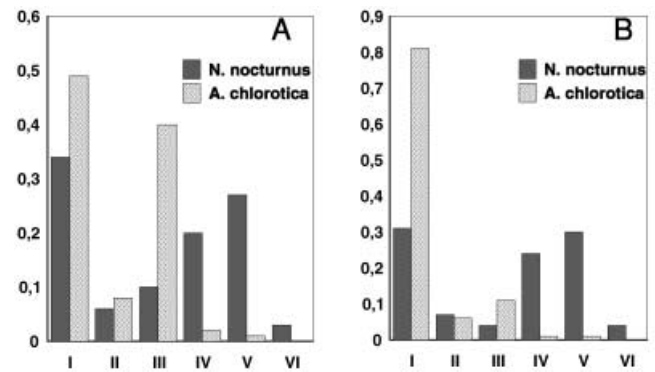


Fig. 3A, B Simulation of behaviour for the two species *N. nocturnus* and *A. chlorotica*. **A** Relative frequency of each kind of movement. **B** Proportion of total moves for each kind of move. I Creating a burrow, II moving forwards before branching off in a lateral burrow, III moving backwards before moving forwards, IV moving forwards before moving backwards, V moving backwards before branching off in a lateral burrow, VI moving forwards before reaching an extremity and digging

Frequencies of behaviours (Fig. 3B) confirmed that *A. chlorotica* burrowed more often than *N. nocturnus* (48% type I and 37%, respectively). The second most frequent behaviour of *A. chlorotica* was a type V movement (44%) but this occurred over short distances (mean=18 mm). Other behaviours (II, III and IV) were rarely displayed by *A. chlorotica* (<8%). Conversely, *N. nocturnus* moved more often in its burrow system: 63% of moves comprising 11% type III, 18% type IV, 26% type V and 3% type VI. The type II movement was relatively infrequent in both species (<5%).

Table 1 Comparison of trajectometry and simulation behaviour in *A. chlorotica* and *N. nocturnus*. Kolmogorov-Smirnov tests between trajectometry and simulation were not significant ($P>0.05$) for either species. *I* Creating a burrow, *II* moving forwards before branching off in a lateral burrow, *III* moving backwards before moving forwards, *IV* moving forwards before moving backwards, *V* moving backwards before branching off in a lateral burrow, *VI* moving forwards before reaching an extremity and digging

Type of movement	<i>A. chlorotica</i>		<i>N. nocturnus</i>	
	Trajectometry (n=156)	Simulation (n=711)	Trajectometry (n=458)	Simulation (n=736)
Percentage of total movement for each kind of move				
I	0.84	0.81	0.21	0.31
II	0.03	0.06	0.18	0.07
III	0.10	0.11	0.04	0.04
IV	0.01	0.01	0.19	0.24
V	0.02	0.01	0.29	0.30
VI	0.00	0.00	0.07	0.04
Relative frequency of movement for each kind of move				
I	0.48	0.49	0.37	0.34
II	0.06	0.08	0.05	0.06
III	0.44	0.40	0.11	0.10
IV	0.01	0.02	0.18	0.20
V	0.02	0.01	0.26	0.27
VI	0.00	0.00	0.03	0.03

Table 2 Transition probabilities between combinations of different kinds of movement obtained by trajectometry (observed) and by simulation for *A. chlorotica* and *N. nocturnus*. For explanation of types of movement, see Table 1

	Trajectometry			Simulation		
	I ^a	III or V	II or IV	I	III or V	II or IV
<i>A. chlorotica</i>						
I ^b	–	0.96	1	–	0.97	1
III or V	0.94	–	0	0.83	–	0
II or IV	0.06	0.04	–	0.17	0.03	–
<i>N. nocturnus</i>						
I	–	0.29	0.86	–	0.24	0.89
III or V	0.93	–	0.14	0.90	–	0.11
II or IV	0.07	0.71	–	0.10	0.76	–

^a Initial movement

^b Subsequent movement

Sequences of behaviour in *A. chlorotica* and *N. nocturnus* also differed (Table 2). *A. chlorotica* had a preferential sequence: (1) creating a burrow (type I); (2) moving backwards (type III or V); (3) creating a burrow (type I); (4) moving backwards (type III or V), etc.; and rarely moving forwards (type II or IV) except when the earthworm met an existing burrow. In *N. nocturnus* the sequence was more varied and earthworms moved many times in their burrow systems thanks to the oscillatory sequence: (1) moving backwards (type III or V), (2) moving forwards (type II or IV), (3) moving backwards (type III or V), etc. Visual inspection showed that the transition probabilities obtained from observed and simulated data were very similar.

Geometrical differences between *A. chlorotica* and *N. nocturnus* burrow systems

The simulated burrow systems built by two virtual species were different (Fig. 2, top). In Table 3, tortuosity (*d*) of the burrow system was higher for *A. chlorotica* than for *N. nocturnus* (*d* is minimal when it equals 1, i.e. when the burrow system only comprises straight burrows). This result means that *A. chlorotica* individuals changed burrowing direction more often than *N. nocturnus*. The difference in sinuosity (*c*) shows that individ-

Table 3 Characteristics of simulated burrow systems

	<i>A. chlorotica</i> (n=286)	<i>N. nocturnus</i> (n=298)	<i>P</i>
Link length (mm) (<i>a</i>)	6.9±0.05	10.5±0.06	0.00
Link incline (degree) (<i>b</i>)	46.5±0.15	52.5±0.17	0.00
Sinuosity (degree) (<i>c</i>)	47.1±0.15	42.2±0.23	0.00
Tortuosity (<i>d</i>)	0.79±0.01	0.85±0.01	0.00
Branching rate (m ⁻¹) (<i>e</i>)	14.0±0.368	11.8±0.24	0.00
Extremity rate (m ⁻¹) (<i>f</i>)	8.9±0.20	7.2±0.10	0.00

Means±95% confidence intervals and comparisons of means (*t*-test probabilities)

uals belonging to *A. chlorotica* changed burrowing direction between two links with a more marked angle. The rate of branching (*e*) of the burrow systems was higher for *A. chlorotica*. Moreover, *A. chlorotica* burrow systems had more extremity nodes (*f*) (dead-ends).

In burrow systems the fluid paths are only a part of the total burrow system (de Dreuzy 2000). Figure 2 (bottom) shows examples of burrow systems for both species in which only the drainage part of the burrow systems (i.e. the part in which the dead-ends were removed) was kept. For *N. nocturnus*, 38% of the total length of the simulated burrow systems was removed against 44% for *A. chlorotica*. Table 4 shows means and confidence limits of characteristics of these burrow

Table 4 Characteristics of the drainage part of the simulated burrow systems

	<i>A. chlorotica</i> (<i>n</i> =286)	<i>N. nocturnus</i> (<i>n</i> =298)	<i>P</i>
Total length of drainage burrow system (<i>g</i>) (m)	2.02±0.07	2.40±0.05	0.00
Rate of branching pipe (<i>h</i>) (m ⁻¹)	6.85±0.32	9.44±0.26	0.00
Number of openings at surface (<i>i</i>)	7.01±0.08	8.14±0.15	0.00
Number of openings at depth (<i>j</i>)	3.05±0.30	5.83±0.13	0.00
Number of independent paths (<i>k</i>)	1.88±0.08	2.71±0.10	0.00
Length of the minimal independent path (<i>l</i>) (m)	0.46±0.02	0.34±0.01	0.00
Mean length of independent paths (<i>m</i>) (mm)	0.53±0.02	0.38±0.01	0.00

Means±95% confidence intervals and comparisons of means (*t*-test probabilities)

Table 5 Multiple linear regressions of permeability (K_{sat}) on geometric parameters characterising burrow systems: value of R^2 of multiple linear regressions: $K_{\text{sat}}=x_1 \times k + x_2 \times (m \text{ or } l) + x_3 \times h + x_4 \times g + x_5 \times i + x_6 \times j + \text{constant}$ for both species with *k*, *m*, *h*, *g*, *i*, *j* and x_1 , x_2 , x_3 , x_4 , x_5 , x_6 the coefficients. Global *P* of *F*-tests and significance level are given for each coefficient. For parameters, see Table 4

R^2	<i>A. chlorotica</i>	<i>N. nocturnus</i>
Total burrow system ^a	0.74 (<i>n</i> =298) (<i>P</i> <0.00)	0.57 (<i>n</i> =286) (<i>P</i> <0.00)
Total burrow system ^b	0.67 (<i>n</i> =298) (<i>P</i> <0.00)	0.63 (<i>n</i> =286) (<i>P</i> <0.00)

^a Path length is *m*

^b Path length is *l*

drainage systems. The first difference between the two species was the total length of drainage (*g*) of their burrow systems. *N. nocturnus* burrow systems displayed a longer final total drainage than *A. chlorotica*. Contrary to the real rate of branching (*e*) (Table 3), the rate of branching pipes (*h*) (i.e. effective interconnectedness) was higher in *N. nocturnus* burrow systems than in those of *A. chlorotica*. Openings at the edges of the space in the simulation (surface and depth limit) were more numerous for *N. nocturnus* than for *A. chlorotica*.

The number of independent paths (*k*) of simulated burrow systems was higher for *N. nocturnus* with a mean of 2.7 independent paths per burrow system, against 1.9 for *A. chlorotica* burrow systems. Furthermore, these independent paths (*m*) were shorter for *N. nocturnus* (0.38 m) than for *A. chlorotica* burrow systems (0.53 m).

Hydrodynamic differences in simulated burrow systems

Permeability at saturation was quite different in the two sets of burrow systems (Table 5). The mean permeability at saturation of *N. nocturnus* burrow systems was higher than those of *A. chlorotica*. These permeability values were high in both cases because of maximal continuity of the simulated burrow. We also noted that in these two sets of burrow systems permeability displayed Gaussian-like distribution.

Table 6 K_{sat} (mean±95% confidence interval) of the simulated burrow systems deduced by: (1) computation of water flow model and two predictions of permeability with (2) ratio of burrow system paths to the length of minimal path (*o*) and (3) ratio of burrow system paths to mean length of paths (*p*). For *P*: *t*-test probabilities for comparisons of means between species. R^2 values for regression of these descriptors with permeability of water flow model are also given

	<i>A. chlorotica</i> (<i>n</i> =286)	<i>N. nocturnus</i> (<i>n</i> =298)	<i>P</i>
(1) Water flow model (10–3 ms ⁻¹)	8.3±0.4	18.9±0.6	0.00
(2) Prediction with <i>o</i> (10–3 ms ⁻¹)	7.9±0.4 ($R^2=0.67$)	14.0±0.6 ($R^2=0.50$)	0.00
(3) Prediction with <i>p</i> (10–3 ms ⁻¹)	6.6±0.3 ($R^2=0.74$)	12.3±0.5 ($R^2=0.54$)	0.00

Multiple linear regressions were performed in order to link permeability (K_{sat}) with geometric parameters that characterise burrow systems (Table 6). The total length of the burrow drainage system (*g*), the rate of branching of the burrow system (*h*) and finally, the number of nodes at the limits of the space (*i*) and (*j*) contributed to a small extent to predicting K_{sat} . Conversely, the number of independent paths (*k*) and their mean length (*m*) best explained the variability of permeability inside a set of burrow systems for each species since percent contribution to variation on K_{sat} , explained by the number of paths and their mean lengths, reached 50% (total of 57%) for *N. nocturnus* burrow systems and 68% (total of 74%) for those of *A. chlorotica*. As the linear regressions showed, the combined descriptors *o* and *p* correctly predicted, the calculated flow deduced from model water flow (Table 6). Moreover, this prediction maintained the significant difference in K_{sat} between the two sets of burrow systems. In the *A. chlorotica* burrow systems, the regression models were markedly improved by classifying them in two groups according to the closest value between the two predicted permeability values [either the ratio with *o* or the ratio with *p*]. Thus, the first group with 91 burrow systems was best explained by *o* ($R^2=0.94$), whereas the second group with 207 burrow systems was best explained by *p* ($R^2=0.77$). This was not the case for *N. nocturnus* burrow systems, since the mean length of the paths was almost equal to the minimal length (Table 4).

Discussion

Difference in behaviour between *A. chlorotica* and *N. nocturnus*

The good agreement between observed data and simulated data confirmed that the model used can correctly simulate the specific behaviour of earthworms. Two specific patterns of behaviour were modelled in the present study: virtual species *A. chlorotica* built burrows more often and of a longer mean length than *N. nocturnus*. On the other hand, *N. nocturnus* moved more frequently in their existing burrow system and mean lengths were longer than those for *A. chlorotica*. Indeed, total building length represented about 80% of movement by *A. chlorotica* versus 31% by *N. nocturnus* which spent more time moving in their existing burrows. These two earthworm species have been taken as representative of the two types of ecological group as defined by Lee and Foster (1991) since endogeic species rarely reuse their burrows whereas anecic species frequently reuse their burrows. To validate general trends between groups, this simulation could test several representative species of each group and take into account the modification in behaviour induced by biophysical soil conditions.

This realistic simulation of earthworm behaviour was able to quantify the dynamics of the creation and use of burrow systems. Even though experimental data are needed, it allows a great number of replicates to be achieved and the variability of earthworm behaviour to be studied using statistical methods. In addition, the impact of different building behaviours of each earthworm species on the final topology of burrow systems can be studied.

Impact of behaviour on the topology of burrow systems

The differences in behaviour between *A. chlorotica* and *N. nocturnus* generated different burrow systems. *A. chlorotica* burrow systems were more interconnected because this species creates a greater number of lateral burrows than *N. nocturnus*. However, the effective interconnectedness (rate of branching of the burrow system where the flow occurs) and the total drainage length of simulated burrow system were not increased. This result could be explained by the numerous branches representing dead-ends that were of no use in calculating steady-state flow. *N. nocturnus* burrow systems had more connectivity than *A. chlorotica*. The higher number of independent paths in *N. nocturnus* burrow systems that connect the top and bottom of the core is probably the consequence of a higher number of nodes at the bottom limit. It is difficult to link this last feature with a particular type of behaviour. However, the higher number of openings for *N. nocturnus* could be explained by the capacity for individuals of this species to elongate all vertical burrows that have already been started, until they reach the bottom of the core. *A. chlorotica* did not give up moving forward and elongated its burrows for a consid-

erable distance. Moreover, *A. chlorotica* changed burrowing direction (tortuosity) and burrowing angle (sinuosity) more sharply than *N. nocturnus*. In the case of *A. chlorotica*, the bottom of the core was reached less often and only after a greater burrowing distance. Consequently, the mean length of independent paths was longer for *A. chlorotica*.

Impact of topology on the permeability of the burrow system

An infiltration model of steady-state flow was made first to study the relationships between burrow systems of different geometry of earthworm species and their permeability at saturation. In the present study, K_{sat} of the two sets of burrow systems was quite different. Regression analyses showed that the number and the length of independent paths throughout the burrow systems were the two essential factors that explained K_{sat} . Indeed, *N. nocturnus* burrow systems displayed higher K_{sat} values than those of *A. chlorotica* because its burrow systems were more connected (i.e. they have more numerous independent paths), and these paths connected the top to the bottom of the core with shorter burrows. These single factors allowed a good approximation of K_{sat} to be predicted from the water flow model. Moreover, even though the diameters of burrows are in reality quite different in these two species this factor would increase the difference in topological permeability in the same way since *N. nocturnus* burrows are bigger than those of *A. chlorotica*.

The relative agreement of predictions with the computed flow gives some information on the paths that control the flow through the burrow system: a single path (i.e. the shortest) or multi-paths (i.e. the total length of the paths) through the burrow system. For *N. nocturnus* the mean length of independent paths is almost the same as the length of the minimal path and consequently the flow through burrow systems of this species is controlled by the whole set of paths. Conversely, the flow through *A. chlorotica* burrow systems is mainly controlled by a single path, the minimal path bypassing the other paths.

The maximal continuity of burrow systems used in this study is an idealistic view of natural burrow systems. This assumption allowed the role of topology to be demonstrated in the absence of refilling. Natural burrow systems are more discontinuous; this variation is due to obstructions caused by the underground casts in burrows, by earthworm burrowing, or by physical degradation of the burrow systems (Hirth et al. 1996; Lighthart and Peek 1997). For this reason, it is probably essential to identify multi-path (in *N. nocturnus*) or conversely, single path (in *A. chlorotica*) water movement throughout the different burrow systems. If the single path of water movement in *A. chlorotica* burrow systems was interrupted by an obstruction, overall flow could show a marked decrease in comparison to the same situation for *N. nocturnus*.

Numerous studies on earthworms have only measured the volume of pore space and the degree of interconnect-

edness (McKenzie and Dexter 1993; Hirth et al. 1996; Lighthart and Peek 1997; Capowiez et al. 1998; Jégou et al. 1998; Langmaak et al. 1999). Our modelling approach leads us to think that these factors are probably not relevant in predicting the permeability of a natural burrow system. It would be necessary to study in more detail the topology and in particular the connectivity of the burrow system as defined by Dullien (1992). This statement could be explained by the fact that total drainage length results from a trade-off: permeability decreases with increasing total drainage length, while permeability increases with the number of independent paths if the total drainage length increases. The total length of a burrow is an even less relevant parameter with which to predict permeability. As total drainage length represents only part of the total length of independent paths, the total length of a burrow does not correspond to the drainage length where flow circulates.

In conclusion, the geometrical data obtained from a burrow system using X-ray computed tomography together with the behavioural data of earthworm using trajectory analysis allowed the creation of a simulation model of earthworm behaviour. In addition to behavioural descriptors (frequencies, distribution of movement length, sequence of behaviours), pore space and topology parameters (burrow length, number of openings, interconnectivity and connectivity) were obtained in the output to characterise simulated burrow systems. Experimental and field data could be multiplied many times using this new tool. The effect of various behaviours on the spatial topology of simulated burrow systems was studied statistically for the two species *A. chlorotica* and *N. nocturnus*.

A functional model like the water flow model can easily be superimposed on simulated burrow systems to generate a hypothesis about the effect of topology on permeability. The best permeability was displayed by *N. nocturnus*. Concerning maximal continuity and constant aperture in a burrow system, our model showed connectivity (number of independent paths) as the best predictor of permeability.

Connectivity was low in the simulated *A. chlorotica* burrow systems because its burrow systems were more tortuous and consequently had fewer independent paths for a given length. Conversely, *N. nocturnus*' burrowing behaviour created more independent paths; these paths connected the surface more directly with the bottom of the core.

Acknowledgements We gratefully acknowledge the technical assistance of Fabrice Harrouet (Enib, Brest) in programming the simulator. We thank M. Lamandé (INRA Rennes – Sciences du sol) for his comments on the manuscript. We thank the two anonymous reviewers for their useful comments.

References

- Beven K, Germann P (1982) Macropores and water flow in soils. *Water Resour Res* 18:1311–1325
- Bouché MB (1977) Stratégies lombriciennes. In: Lohm U, Persson T (eds) Soil organisms as components of ecosystems. *Ecol Bull (Stockh)* 25:122–132
- Bouma J (1991) Influence of soil macroporosity on environmental quality. *Adv Agron* 46:1–37
- Capowiez Y (2000) Differences in burrowing behaviour and spatial interaction between the two earthworm species *Aporrectodea nocturna* and *Allobophora chlorotica*. *Biol Fertil Soils* 30:341–346
- Capowiez Y, Belzunces L (2001) Dynamic study of the burrowing behaviour of *Aporrectodea nocturna* and *Allobophora chlorotica*: interactions between earthworms and spatial avoidance of burrows. *Biol Fertil Soils* 33:310–316
- Capowiez Y, Pierret A, Daniel O, Monestiez P, Kretzschmar A (1998) 3D skeleton reconstructions of natural earthworm burrow system using CAT scan images of soil cores. *Biol Fertil Soils* 27:51–59
- Capowiez Y, Monestiez P, Belzunces L (2000a) Burrow system made by *Aporrectodea nocturna* and *Allobophora chlorotica* in artificial cores: morphological differences and effects of interspecific interactions. *Appl Soil Ecol* 16:109–120
- Capowiez Y, Pierret A, Monestiez P, Belzunces L (2000b) Evolution of burrow systems after the accidental introduction of a new earthworm species into a Swiss pre-alpine meadow. *Biol Fertil Soils* 31:394–500
- Daniel O, Kretzschmar A, Capowiez Y, Kholi L, Zeyer J (1997) Computer-assisted tomography of macroporosity and its application to study the activity of the earthworm *Aporrectodea nocturna*. *Eur J Soil Sci* 48:727–737
- Dreuzy JR de (2000) Analyse des propriétés hydrauliques des réseaux de fractures. Discussion des modèles d'écoulement compatibles avec les principales propriétés géométriques. Mémoires n°94. Department of Geosciences, University of Rennes, Rennes
- Dullien FAL (1992) Porous media – fluid transport and pore structure, 2nd edn. Academic Press, New York
- Edwards WM, Shipitalo MJ, Owens LB, Norton LD (1990) Effects of *Lumbricus terrestris* burrows on hydrology of continuous no-till corn fields. *Geoderma* 46:73–84
- Ela SD, Gupta SC, Rawls WJ (1992) Macropore and surface seal interaction affecting water infiltration into soil. *Soil Sci Soc Am J* 56:714–721
- Elhers W (1975) Observations on earthworm channels and infiltration on tilled an untilled loess soil. *Soil Sci* 119:242–249
- Ferber J (1995) Les systèmes multi-agents: vers une intelligence collective. InterEditions, Paris
- Francis GS, Fraser PM (1998) The effects of three earthworm species on soil macroporosity and hydraulic conductivity. *Appl Soil Ecol* 10:11–19
- Hirth JR, McKenzie BM, Tisdall JM (1996) Volume density of earthworm burrows in compacted cores of soil as estimated by direct and indirect methods. *Biol Fertil Soils* 21:171–176
- Jégou D, Cluzeau D, Wolf HJ, Gandon Y, Trehen P (1998) Assessment of the burrow system of *Lumbricus terrestris*, and *Aporrectodea caliginosa* using X-ray computed tomography. *Biol Fertil Soils* 26:116–121
- Jégou D, Hallaire V, Cluzeau D, Trehen P (1999) Characterization of the burrow system of earthworms *Lumbricus terrestris* and *Aporrectodea giardi* using X-ray computed tomography and image analysis. *Biol Fertil Soils* 29:314–318
- Joschko M, Graff O, Muller PC, Kotzke K, Lindner P, Pretschner DP, Larink O (1991) A non-destructive method for the morphological assessment of earthworm burrow system in three dimensions by x-ray computed tomography. *Biol Fertil Soils* 11:88–92
- Joschko M, Sochtig W, Larink O (1992) Functional relationship between earthworm burrows and soil water movement in column experiments. *Soil Biol Biochem* 24:1545–1547
- Judson OP (1994) The rise of the individual-based model in ecology. *Trends Ecol Biol* 9:9–14
- Knight D, Elliot PW, Anderson JM, Scholefield P (1992) The role of earthworms in managed, permanent pasture in Devon, England. *Soil Biol Biochem* 24:1511–1517
- Langmaak M, Shrader S, Rapp-Bernhardt U, Kotzke K (1999) Quantitative analysis of earthworm burrow systems with respect to biological soil-structure regeneration after soil compaction. *Biol Fertil Soils* 28:219–229

- Lee KE (1985) Earthworms their ecology and relationships with soils and land use. Academic Press, Sydney
- Lee KE, Foster RC (1991) Soil fauna and soil structure. *Aust J Soil Res* 29:745–775
- Ligthart TN, Peek GJCW (1997) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in The Netherlands. *Soil Biol Biochem* 29:453–462
- MacDonald IF, Kaufmann PM, Dullien AL (1986) Quantitative image analysis of finite porous media. I. Development of genus and pore map software. *J Microsc* 144:297–296
- Martin S, Lavelle P (1992) A simulation model of vertical movements of an earthworm population (*Millsonia anomala* Omodeo, Megascolidae) in an African savannah (Lamto, Ivory coast). *Soil Biol Biochem* 24:1419–1424
- McCoy EL, Boast CV, Stehouver RC, Kladivko EJ (1994) Macropore hydraulics: taking a sledgehammer to classical theory. In: Lal R, Stewart A (eds) *Soil processes and water quality*. Lewis, Boca Raton, Fla. pp 303–348
- McKenzie BM, Dexter AR (1993) Size and orientation of burrows made by earthworms *Aporrectodea rosea* and *A. caliginosa*. *Geoderma* 56:233–241
- Monestiez P, Kretzschmar A (1992) Estimation of the relationship between structural parameters of simulated burrow systems and their partitioning effect. *Soil Biol Biochem* 24:1549–1554
- Munyankusi E, Gupta SC, Moncrief JF, Berry EC (1994) Earthworm macropores and preferential transport in a long term manure applied typical hapludalf. *J Environ Qual* 23:773–784
- Perrier E (1995) Structure géométrique et fonctionnement hydrique des sols. Simulations exploratoires. Thèse d'état. Orstom, Paris
- Pitkanen J, Nuutinen V (1995) Soil macropores, saturated hydraulic conductivity and earthworm activity on two soils under long-term reduced tillage in southern Finland. *Acta Zool Fenn* 196:251–253
- Robinson PC (1983) Connectivity of fracture systems. A percolation theory approach. *J Phys A* 16:605–614
- Smetten KJR (1992) The relation of earthworms to soil hydraulic properties. *Soil Biol Biochem* 24:1539–1543
- Smetten KJR, Collis-George N (1985) The influence of cylindrical macropores on steady-state infiltration in a soil under pasture. *J Hydrol* 79:115–122
- Stockdill SMJ (1982) Effect of introduced earthworms on productivity of New Zealand pasture. *Pedologie* 24:29–35
- Spanne P, Thovert JF, Jacquin CJ, Lindquist WB, Jones KW, Adler PM (1994) Synchrotron computed microtomography of porous media: topology and transports. *Phys Rev Lett* 73:2001–2004
- Urbanek J, Dolezal F (1992) Review of some cases studies on the abundance and on the hydraulic efficiency of earthworm channels in Czechoslovak soils, with reference to the subsurface pipe drainage. *Soil Biol Biochem* 24:1563–1571
- Zachmann JE, Linden DR, Clapp CE (1987) Macroporous infiltration and redistribution as affected by earthworms, tillage and residue. *Soil Sci Soc Am J* 51:1580–1586