



# Soil micropore structure and carbon mineralization in burrows and casts of an anecic earthworm (*Lumbricus terrestris*)

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Received 22 June 1999; received in revised form 8 February 2001; accepted 8 March 2001

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## Abstract

Anecic earthworms (those that build semipermanent vertical burrows) are known to alter the biological activity and physical structure of soils through their burrowing and casting. Information on how earthworms change the physical structure of soil may provide clues about the mechanisms by which earthworms affect microbial processes such as nutrient mineralization. We evaluated the pore structure of bulk soil and of the soil in burrows and casts formed by an anecic species of earthworm (*Lumbricus terrestris*) in a fallow field. Differences in pore structure (specific pore volume,  $V_{sp}$ , and median pore neck dia.,  $D$ ) were assessed using mercury intrusion porosimetry. We also examined the relationship of these physical properties with mass water content at field capacity ( $\theta_m$ ), rate of C mineralization ( $C_{min}$ ) and specific C mineralization rate ( $C_{sp} = C_{min}/C$  content of soil). Mean values of  $V_{sp}$  ( $\pm$ SD) for bulk, cast and burrows were  $242 \pm 35$ ,  $213 \pm 13$ , and  $197 \pm 4 \mu\text{l g}^{-1}$ , respectively. Values for  $D$  were ( $\pm$ SD)  $10.8 \pm 2.5$ ,  $7.9 \pm 3.3$ , and  $5.5 \pm 2.9 \mu\text{m}$  for bulk, burrow, and cast soil, respectively. A smaller proportion of the pore volume in cast and burrow soil was associated with pore diameters in the 3–30 and 30–100  $\mu\text{m}$  range than in bulk soil.  $\theta_m$  was higher in burrow and cast soil than in bulk soil and was inversely proportional to  $V_{sp}$  and  $D$ .  $C_{min}$  and  $C_{sp}$  followed the order: burrow > cast > bulk soil. Both  $C_{min}$  and  $C_{sp}$  decreased inversely with  $V_{sp}$ . By contrast, no consistent relationship was observed between either measure of C mineralization and  $D$ . Our results suggest that the changes in soil pore structure produced by anecic earthworms cause a shift towards smaller pore volume and smaller pore neck diameters. These changes in turn affect physical (e.g. water retention) and microbial (e.g. C mineralization) processes in soil. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Anecic earthworms; *Lumbricus terrestris*; C mineralization; Pore structure; Drilosphere; Casts

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## 1. Introduction

The pore structure of soil is a basic constraint on soil ecosystems because it controls nutrient and water fluxes, water availability, gas diffusion, and habitat for soil organisms. Pore structure is a dynamic soil property that can be altered by tillage and traffic, root growth, and burrowing of soil animals. The resulting alterations in habitable pore space affect the soil ecosystem because habitable pore space controls the structure, function, and interaction of microbial and microfaunal communities in soil (Darbyshire, 1976; Elliott et al., 1980; Hassink et al., 1993). The effects of pore structure on soil biota have been observed for a wide range of pore diameters. For example, the population density of microarthropods was positively correlated with pores of diameters  $>90 \mu\text{m}$  and negatively correlated with pores of diameter  $<1.2 \mu\text{m}$  (Vreeken-Bujis et al., 1998). Pore sizes in the order of  $1 \mu\text{m}$  were correlated positively

with the bacterial biomass, whereas nematodes were correlated with pore diameters of 30–90  $\mu\text{m}$  (Hassink et al., 1993). Kilbertus (1980) suggested a limit of 0.2  $\mu\text{m}$  pore diameter for access of microorganisms to pore spaces.

Earthworms affect the pore structure of soil through burrowing and casting (Kretzschmar, 1978; Lavelle, 1997). In particular, qualitative micromorphological analysis suggests that drilosphere soil contains smaller pores, and less overall porosity, than the bulk soil (Kretzschmar, 1987; West et al., 1991; Binet and Curmi, 1992) due to soil compression or selective ingestion of smaller soil particles by earthworms. Anecic earthworms also line their burrows with cast material (Jeanson, 1979; Kretzschmar, 1987; Binet and Curmi, 1992) and aggregates formed from casts have greater stability than bulk soil, suggesting structural or chemical differences between bulk and cast soils (Shipitalo and Protz, 1989; Ziegler and Zech, 1992; Zhang and Schrader, 1993). Earthworm casts also exhibit greater moisture retention capacity (Ziegler and Zech, 1992; Zhang and Schrader, 1993; Devliegher and Verstraete, 1997) than bulk soil. The discontinuity created by differences in pore

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sizes between either drilosphere or cast soil and bulk soil can impede movement of water and nutrients from the burrow lining to the adjacent soil (West et al., 1991; Binet and Curmi, 1992). These physical differences may influence ecological processes at the local (e.g. burrow) and landscape scales. For example, cast and drilosphere soil generally contain larger microbial populations (Tiwari et al., 1989; Tiwari and Mishra, 1993), and exhibit higher nutrient mineralization rates (Tiwari et al., 1989) than bulk soil.

Our aim was to quantify changes in the distribution of pore sizes and pore volume caused by anecic earthworms under field conditions. This would complement previous, qualitative data on soil pore structure (e.g. West et al., 1991; Binet and Curmi, 1992). We measured the pore structure of burrow, bulk and cast soils using mercury intrusion porosimetry (Webb and Orr, 1997) to quantify physical changes in habitat—pore diameter and volume—at scales relevant to soil microflora and fauna (100 nm to 100  $\mu\text{m}$ ) (Elliott and Coleman, 1988). We tested the hypothesis that differences in physical structure produced by anecic earthworms affect C mineralization (Görres et al., 1997). We measured soil moisture, C mineralization, and total C and N content for these soils to quantify the relationships between soil micropore structure, moisture retention, and C mineralization.

## 2. Materials and methods

### 2.1. Study area and sampling

Soil samples were collected in May 1998 from a fallow corn field at the Peckham Farm Research Area of the University of Rhode Island in Kingston, RI, USA. The field was last planted to corn in 1995 and not cultivated since then. The soil is an Enfield silt loam (coarse-silty over sandy or sandy-skeletal mesic Typic Dystrudept) (Soil Survey Staff, 1981) with a pH of 5.0, an organic matter content of 35 mg g<sup>-1</sup> soil, and a C-to-N ratio of 15. The soil had been saturated by 2.5 cm of rainfall 2 days prior to sample collection. To estimate the variance in pore structure of cast and burrow soil, three points (separated by about 2 m) were selected from a 15 × 15 m plot and at each point a sample of drilosphere, bulk and cast soil were collected. Soil samples were collected exclusively from burrows for which we could confirm occupancy by live *L. terrestris* through visual inspection. Drilosphere soil was identified as soil that was in contact with an earthworm and showed a worm imprint. We sampled drilosphere soil by scraping and collecting the soil less than 5 mm away from the inner boundary of the burrow. Drilosphere soil was kept separate from bulk and cast soil. Casts were removed from the surface next to the burrow entrance. Bulk soil was taken 5 cm away from any surface casts or burrows. Burrow and bulk soil samples were obtained from the top 10 cm of soil.

### 2.2. Characterization of pore structure

Mercury intrusion porosimetry measures pore size distribution in porous solids. It has been applied successfully to soils (Lawrence, 1978; Pachepsky et al., 1995) without altering the soil pore structure, despite the high pressures generated (Lawrence, 1978). The method involves forcing mercury into soil samples at given capillary pressures. The volume of mercury intruded at a given pressure gives the pore volume that can be accessed through pore necks that are penetrated at the intrusion pressure. By increasing pressure stepwise and allowing mercury intrusion to reach equilibrium between each step, a pore size distribution can be obtained. It is important to interpret mercury porosimetry data considering the characteristics of the pore structure of the material investigated. We interpreted pore size distributions with a simple pore network model which does not assume any particular pore geometry (Webb and Orr, 1997). This model assumes the following.

- Intrusion occurs through constrictions of hydraulic diameter,  $D$ .
- The pore neck diameter is given by  $D = A/P$ , where  $A$  is the cross-sectional area of a pore neck and  $P$  is the cross-sectional perimeter.
- Pore size distribution with mercury porosimetry gives pore volume accessible through constrictions of diameter  $D$ , and not the frequency of pores of that size.

The model yields two types of information from the pore size distribution obtained with mercury porosimetry: (1) the diameter ( $D$ ) of pore necks, which control intrusion of mercury into pore chambers accessible through the necks, and (2) the combined volume of pore necks and pore chambers ( $V_{\text{sp}}$ ). This model assumes that pore neck diameter,  $D$ , and volume of pore chambers are not related by any particular geometric function. Thus, small or large intrusion volumes in any given pore neck diameter range may represent either small or large linear chamber sizes (i.e. average distance between pore walls) regardless of pore neck diameter.

Soil samples were prepared for porosimetry by drying in an evacuated desiccator overnight at room temperature. A known mass (about 0.8 g) of each desiccated sample was placed into a powder penetrometer. Prior to filling the penetrometer with mercury, the sample was evacuated to an absolute pressure of 3 Pa. Intrusion volumes were measured at 25 increasing pressures ranging from  $2 \times 10^0$  to  $5 \times 10^5$  kPa (equivalent to 100–0.05  $\mu\text{m}$  pore neck diameters) using an AutoPore 9420 porosimeter (Micromeritics). Samples were allowed to equilibrate for 3 min (determined empirically to be the optimal time) at each target pressure before the intrusion volume was measured. All the necessary precautions were taken to minimize exposure of workers to mercury during the course of analysis. Mercury did not come in contact with the atmosphere while the porosimeter was

operating, and the instrument was kept in a well-ventilated area. Sources of mercury were sealed during storage and all transfers were made under a fume hood. Exposure to mercury was further prevented by wearing protective clothing, goggles and gloves. Specific intrusion volumes (volume of mercury intruded per unit weight of sample) were corrected for the moisture content of the desiccated samples (determined from an aliquot of the samples). Total specific intrusion volume was taken as the volume that had intruded at  $5 \times 10^5$  kPa. We derived intrusion pore diameters from intrusion pressure values using the Washburn equation (Washburn, 1921). Pore size distributions were obtained by plotting the intrusion volumes against intrusion diameters. The median pore size diameter was taken from this distribution at the point where 50% of the sample pore space was filled with mercury.

To analyze which pore size intervals contributed to the differences between bulk, burrow and cast porosities, we compared the intrusion volumes for pore neck diameters in the intervals from  $<0.3$ ,  $0.3$ – $3$ ,  $3$ – $30$ , and  $30$ – $100$   $\mu\text{m}$ . These intervals correspond to pore necks that are considered inaccessible to bacteria ( $<0.3$   $\mu\text{m}$ ), in which bacteria are protected from predation ( $0.3$ – $3$   $\mu\text{m}$ ) (Postma and van Veen, 1990), where protozoa can access their prey ( $3$ – $30$   $\mu\text{m}$ ) (Darbyshire, 1976), and where nematodes can access their prey ( $30$ – $100$   $\mu\text{m}$ ) (Hassink et al., 1993).

For one replicate set of soil samples we measured bulk density using mercury pycnometry. The volume of the penetrometer was derived from the weight of mercury that filled the penetrometer at 3 Pa. A desiccated soil sample of known, oven-dry weight was then placed in the penetrometer, which was subsequently filled with mercury at 3 Pa. The volume of mercury that filled the penetrometer containing the sample was calculated from the weight of mercury. The sample volume was computed as the difference between volume of mercury in the penetrometer with or without the sample. The sample weight divided by the difference in volume of mercury gave the sample bulk density.

### 2.3. Water content

Soil water content ( $\theta_m$ ) was determined gravimetrically from the differences in weights of oven-dried soil (24 h at  $105^\circ\text{C}$ ) and fresh samples. We took the resulting value of  $\theta_m$  to be representative of water held at field capacity for bulk, burrow, and cast soil. We based this on the fact that a precipitation event leading to soil saturation occurred 2 days prior to field sampling and that no precipitation fell subsequently. We did not know the history of burrow formation or cast deposition for the samples used in our study. However, it seems reasonable to assume that, whether these structures were in place prior to the rain event or elaborated subsequent to it, the soil in the structures was saturated and allowed to drain for 2 days under field condi-

tions, consistent with the generally accepted definition of field capacity (e.g. Brady and Weil, 1996).

### 2.4. Carbon mineralization and C and N content of soil

Carbon mineralization rates were determined by gas chromatographic analysis following static incubation of samples. Immediately after collection a sample of soil (2 g) was placed in a 20-ml glass serum vial, the vial stoppered with a rubber septum and crimped with an aluminum collar. The sealed vials were incubated in the dark at field soil temperature ( $15^\circ\text{C}$ ) for 4 days. At the end of the incubation, the concentration of  $\text{CO}_2$  in the headspace of the vial was determined. A 1.0-ml sample of the gases in the glass vial was removed by displacement with  $\text{H}_2$  using an automated headspace sampler (model 7000, Tekmar). The concentration of  $\text{CO}_2$  in the sample was measured with a gas chromatograph (model 14A, Shimadzu) fitted with a Porapak Q column (80/100 mesh, 305 cm). Carbon dioxide was converted to  $\text{CH}_4$  using a heated ( $400^\circ\text{C}$ ) Ni catalyst and an  $\text{H}_2$  gas stream, and the resulting  $\text{CH}_4$  measured with a flame ionization detector. Injector, column and detector temperatures were 150, 60 and  $300^\circ\text{C}$ , respectively. Peak areas for  $\text{CO}_2$  were determined by electronic integration. Conversion of peak areas to mass of  $\text{CO}_2$  was made by comparison with vials containing a known concentration of  $\text{CO}_2$ .

Total C and N content of soil was determined using an automated nitrogen/carbon analyzer (model NA 1500/ Series 2, Carlo Erba).

### 2.5. Statistical analyses

Statistical comparisons of the properties of burrow and cast soil with bulk soil were made using Student's two-tailed test. Differences in intrusion volume for different pore size ranges among burrow, cast and bulk soil were assessed using a one-way analysis of variance. Multiple comparisons were made using the Student–Newmann–Keuls method.

## 3. Results

### 3.1. Soil pore structure

Bulk soil was the most porous and burrow soil the least porous, as indicated by mean values of specific pore volume,  $V_{\text{sp}}$  (the volume of Hg intruded per unit weight of sample) (Table 1). Values of  $V_{\text{sp}}$  for all soil samples were lower than expected from the porosity and bulk density data for the Enfield silt loam. However, the analysis we performed gives greater emphasis to aggregate than inter-aggregate spaces. Bulk density for this soil is  $1.3 \text{ g cm}^{-3}$  measured using undisturbed cores (vol. = 100 ml) (data not shown). Pycnometric analysis gave densities of  $1.6 \text{ g cm}^{-3}$  (bulk and burrow soil) and  $1.7 \text{ g cm}^{-3}$  (cast soil).

Table 1  
Total C and N content, C mineralization rates, moisture, and pore structure parameters for bulk, burrow, and cast soil. Values are mean  $\pm$  SD ( $n = 3$ ). Significantly different from bulk soil: \* $P < 0.10$ , \*\* $P < 0.05$

Soil	$C_{\text{tot}}$ ( $\text{mg g}^{-1}$ )	$N_{\text{tot}}$ ( $\text{mg g}^{-1}$ )	C-to-N ratio	$C_{\text{min}}$ ( $\mu\text{g CO}_2\text{-C g}^{-1} \text{d}^{-1}$ )	$C_{\text{sp}}$ ( $\mu\text{g CO}_2\text{-C mg C}^{-1} \text{d}^{-1}$ )	$\theta_m$ (%)	$V_{\text{sp}}$ ( $\mu\text{l Hg g}^{-1}$ )	$D$ ( $\mu\text{m}$ )
Bulk	$17.6 \pm 3.9$	$1.2 \pm 0.2$	$14.9 \pm 1.1$	$10.8 \pm 2.8$	0.61	$17.8 \pm 3.0$	$242 \pm 35$	$10.8 \pm 2.5$
Burrow	$15.9 \pm 2.5$	$1.2 \pm 0.2$	$13.5 \pm 0.4$	$40.8 \pm 11.0^{**}$	2.56	$23.1 \pm 6.3$	$197 \pm 4^*$	$7.9 \pm 3.3$
Cast	$16.8 \pm 1.9$	$1.1 \pm 0.1$	$15.4 \pm 1.1$	$31.2 \pm 8.0^{**}$	1.86	$22.5 \pm 2.2^{**}$	$213 \pm 13$	$5.5 \pm 2.9^*$

The greater densities measured with pycnometry can be attributed to the scale at which measurements are made, which emphasizes aggregate over interaggregate pore volume, and is reflected in the lower than expected  $V_{\text{sp}}$  measured.

The reduction in  $V_{\text{sp}}$  that occurred when soils were altered by the activity of earthworms was accompanied by a reduction in the average of the median pore neck diameter,  $D$ , through which pore volumes can be accessed.  $D$  for burrow soil was one third less than for bulk soil and two times lower in cast than in bulk soil. However,  $V_{\text{sp}}$  and  $D$  were not linearly correlated ( $r^2 = 0.677$ ;  $P = 0.455$ ). Reduction of specific pore volume probably results from radial compression of soil as it passes through the gut or through compression of soil as a result of displacement of soil particles from burrowing. While both of these mechanisms are expected to result in smaller pore diameters, the relationship between  $V_{\text{sp}}$  and  $D$  may not be linear, since it is governed by pore geometry.

Intrusion pore volume was greater for the bulk than for the cast and burrow soil in the 3–30 and 30–100  $\mu\text{m}$  pore diameter intervals, but less for the bulk soil than in the cast and burrow soil in the 0.3–3  $\mu\text{m}$  range (Fig. 1). ANOVAs performed within each pore size interval showed that there were statistically significant differences in intrusion volumes between soils only for the pore diameter interval 30–100  $\mu\text{m}$  ( $P < 0.002$ ). A means separation test (Student–Newmann–Keuls method) showed that in this interval the intrusion volume of cast soil was significantly smaller than in the burrow soil ( $P < 0.002$ ) and that the intrusion volume of the burrow soil was less than that of the bulk soil ( $P < 0.011$ ).

### 3.2. Carbon mineralization in relation to soil pore structure

Carbon mineralization was evaluated in two ways: (1) as the amount of  $\text{CO}_2$  released  $\text{d}^{-1}$  relative to the mass of soil

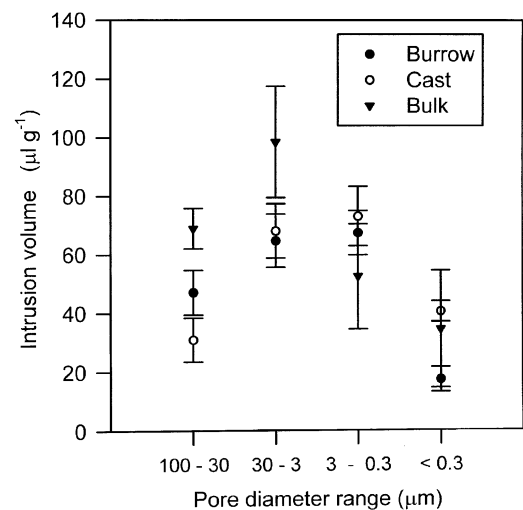


Fig. 1. Intrusion volume for burrow, cast and bulk soil for different pore neck diameter ( $D$ ) ranges. Mean ( $n = 3$ ) values are shown. Bars represent 1 SD.

(designated  $C_{min}$ ) and (2) as the amount of  $CO_2$  released  $d^{-1}$  relative to total pool of soil carbon (designated  $C_{sp}$ ). The former value is reported more commonly and allows comparison with previous studies. The latter value provides an indication of how biologically active the soil organic C pool is.  $C_{min}$ ,  $C_{sp}$ , and  $\theta_m$  were highest in burrow soil, lower in cast soil, and lowest in bulk soil (Table 1). Both  $C_{min}$  and  $C_{sp}$  were correlated linearly with  $\theta_m$  (Fig. 2). By contrast, we did not observe a consistent linear relationship between the soil C-to-N ratio and either  $C_{min}$  ( $r^2 = 0.305$ ;  $P = 0.627$ ) or  $C_{sp}$  ( $r^2 = 0.346$ ;  $P = 0.599$ ).

Soil pore structure is thought to be an important control on the activities and interactions of the microflora and microfauna (e.g. Hassink et al., 1993). As such, we evaluated the relationship between carbon mineralization ( $C_{min}$  and  $C_{sp}$ ) and pore neck diameter ( $D$ ) and  $V_{sp}$ . A significant, negative linear relationship was observed between both  $C_{min}$  and  $C_{sp}$ , and  $V_{sp}$  (Fig. 2). By contrast, no significant linear relationship was apparent between either measure of C mineralization and  $D$  (Fig. 2).

#### 4. Discussion

Our results show that burrow soil and casts generated by anecic earthworms are markedly different from bulk soil in terms of C mineralization, water content, and pore size distribution. Others (e.g. Stehower et al., 1994; Görres et al., 1997; Devliegher and Verstraete, 1997) have shown that C mineralization and moisture content are higher in burrow and cast soil than in burrow soil. Our data allow us to evaluate these effects in the context of measured changes in the pore structure of soil.

##### 4.1. C mineralization in cast, burrow, and bulk soil

Values for  $C_{min}$  and  $C_{sp}$  were highest in burrow soil,

followed by cast and bulk soil (Table 1). By contrast, there were no statistically significant differences in  $C_{tot}$  among bulk, cast and burrow soil (Table 1). The absence of differences in  $C_{tot}$  among cast, burrow, and bulk soil may be the result of fine-scale spatial variability of organic matter distribution in bulk soil (cf. Amador et al., 2000). Increases in  $C_{min}$  and  $C_{sp}$  in burrow and cast soil were disproportionately higher than expected from differences in the soil organic C content of these soils. These results are thus contrary to the general expectation of C mineralization rates controlled by soil organic carbon content (e.g. Alef, 1995). The differences in  $C_{min}$  and  $C_{sp}$  could not be attributed to differences in substrate quality, since the C-to-N ratio of these soils was not significantly different (Table 1). Greater C mineralization activity relative to the pool of organic C may result from differences in the proportion of mineralizable C in bulk vs. burrow and cast soil, and a larger or more active microbial community in the structures created by earthworms. Differences in  $C_{sp}$  between burrow and cast soil may be explained by differences in the dynamics of C inputs into these structures. Burrows receive a relatively frequent input of mineralizable organic C in the form of mucus and through litter translocation. By contrast, there are no external inputs of organic C into cast soil once it is deposited, resulting in a diminishing pool of mineralizable C with time. Differences in the size and composition of the microbial community between cast and burrow soil may also contribute to differences in  $C_{sp}$ .

##### 4.2. Relationship between pore size distribution and soil moisture

The partitioning of pore volume towards smaller pore necks resulting from earthworm activities is a factor in the greater moisture values we observed for burrow soil. When burrow and bulk soil are at a similar water content, the

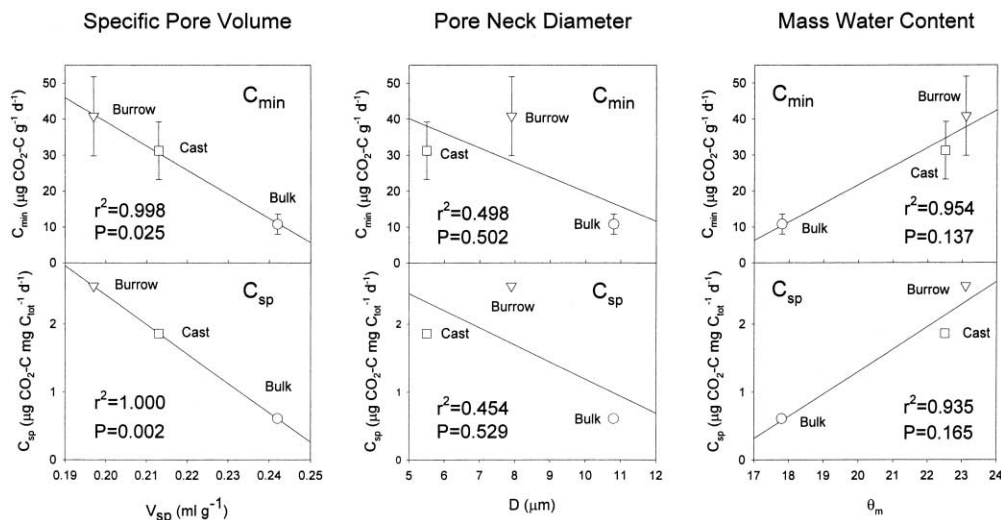


Fig. 2. Relationship between C mineralization ( $C_{min}$  and  $C_{sp}$ ) and specific pore volume ( $V_{sp}$ ), mean pore diameter ( $D$ ), and mass water content ( $\theta_m$ ) in bulk, burrow and cast soil.

burrow soil has a lower matric potential than the bulk soil. Under these conditions water moves from the bulk soil into the drilosphere. When the matric potentials are the same (hydrologically equilibrated condition), more water is held in the drilosphere because a greater portion of pore space is associated with smaller pore necks in the drilosphere. A directional bias of unsaturated water flow from bulk to burrow soil has been observed by others. For example, Stehower et al. (1994) suggested that lateral flow from the bulk into burrow soil may account for some of the increased concentration of herbicides found in burrow soil. Similar processes may play a role in the water dynamics of earthworm casts. However, there is likely to be a greater hydrologic disconnection between cast and bulk soil because there is less contact between them, resulting in less diffusion of dissolved organic C between casts and bulk soil.

#### 4.3. C mineralization in relation to soil pore structure

The linear relationship between measures of carbon mineralization ( $C_{\min}$  and  $C_{\text{sp}}$ ) and  $V_{\text{sp}}$  may be a function of changes in pore chamber sizes associated with diminishing specific pore volume (Table 1, Fig. 1). This can result in concentration of resources and primary and secondary consumers in smaller volumes, making interactions more efficient. A greater proportion of the water is held in the smaller pores in cast and burrow soil, and bacteria reside preferentially in smaller, water-filled pores (Kilbertus, 1980; Hassink et al., 1993). In addition, a linear relationship was observed between  $C_{\min}$  and  $C_{\text{sp}}$  and  $\theta_m$  (Fig. 2) and  $\theta_m$  and  $V_{\text{sp}}$ . Together, these results suggest that the effects of pore structure on C mineralization are associated closely with specific pore volume and the size of pores in which water is held, and not the diameter of pore necks ( $D$ ) through which pores can be accessed, because there was no apparent relationship between  $C_{\text{sp}}$  and  $D$ . Our results indicate that pore neck diameter, often regarded as the physical dimension in the soil that separates niches of microfauna and microflora (Ettema, 1998) may not be as important to explain  $C_{\min}$  and  $C_{\text{sp}}$  as the volume of pores associated with a particular pore size.

Our results are consistent with the enclosure hypothesis proposed by Görres et al. (1999). This hypothesis predicts that, as soil water drains from interaggregate spaces, aggregates (because they have pore size distributions that are small relative to interaggregate spaces) remain sufficiently wet to support the microflora and microbivorous fauna, such as nematodes and protozoa. This would explain our findings that  $D$  does not correlate with  $C_{\min}$ : Görres et al. (1999) have observed that simple pore neck diameters do not explain the presence or absence of nematodes in soil. However, a reduction in available pore volume (habitat) would bring soil microfauna and microflora into closer proximity, which in turn results in enhanced amounts of C and nutrient mineralization. Cast and burrow soil may thus be thought of as

hydrologically isolated enclosures where ecological interactions and biogeochemical processes are accelerated.

The high degree of statistical significance observed for differences in variables among bulk, burrow, and cast soil—as well as for relationships among physical and biological properties—underscores the strength of the effects that anecic earthworms have on soil micropore structure and C mineralization. The mechanisms involved in exerting these effects may include greater numbers of bacteria in water-filled pores, higher concentrations of C and energy sources and nutrients, or stimulation of bacterial activity through grazing by microbivorous soil fauna, all of which could be enhanced by water retention in pores with smaller necks.

#### 4.4. Conclusions

Our results indicate that anecic earthworms cause measurable, statistically significant changes in the pore structure of soil through burrowing and casting. Under field conditions these changes occur at a scale (100 nm–100  $\mu\text{m}$ ) relevant to microflora and fauna. Furthermore, we have shown that there is a very strong relationship between changes in pore structure and C mineralization. Specifically, the resulting shift in pore structure to smaller pores results in enhanced water retention and appears to have a strong, positive effect on C mineralization. The shift in soil pore size distribution caused by the activities of anecic earthworms may constitute an important control on the ecological interactions and biogeochemical processes that take place in soil affected by these organisms.

#### Acknowledgements

Support for this study was provided by the U.S. Department of Agriculture National Research Initiative Competitive Grants Program, by the Rhode Island Agricultural Experiment Station, and by the author's personal funds. We thank an anonymous reviewer for helpful suggestions to improve the manuscript.

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