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Earthworm burrowing in laboratory microcosms as influenced by soil temperature and moisture

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Summary

Earthworm burrows contribute to soil macroporosity and support diverse microbial communities. It is not well known how fluctuations in soil temperature and moisture affect the burrowing activities of earthworms. The objective of this experiment was to evaluate the maximum depth and length of burrows created by the endogeic earthworm *Aporrectodea caliginosa* (Savigny) and the anecic earthworm *Lumbricus terrestris* L. for a range of temperatures (5–20 °C) and soil water potentials (−5 and −11 kPa). The laboratory microcosm was a plexiglass chamber (45 cm high, 45 cm wide) containing 0.14 m^2 of pre-moistened soil and litter, designed to house a single earthworm for 7 days. Earthworm mass, surface casting and burrowing activities were affected significantly by soil temperature, moisture and the temperature-moisture interaction. Burrow length and maximum burrow depth increased with increasing temperature, but there was less burrowing in wetter soil (−5 kPa) than drier soil (−11 kPa). Weight gain and surface casting, however, were greater in soil at −5 kPa than −11 kPa. Our results suggest more intensive feeding and limited burrowing in wetter soil than drier soil. Earthworms inhabiting the non-compacted, drier soil may have pushed aside particles without ingesting them to create burrows. The result was that earthworms explored a larger volume of soil, deeper in the chamber, when the soil was drier. How these burrowing activities may affect the community structure and activity of soil microorganisms and microfauna in the drilosphere remains to be determined.

Introduction

Earthworm burrows function as soil macropores, thus influencing water infiltration and aeration.

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While burrows may improve the structure of compacted and tilled agricultural soils (Kladivko, 2001; Langmaack et al., 2002), they also function as preferential flow pathways for pesticide and nutrient transport (Edwards et al., 1993; Shuster et al., 2003). Burrow walls are enriched in organic matter and support a unique and active community of microflora and microfauna, compared to the surrounding soil (Gorres et al., 1997; Tiunov and Scheu, 1999; Jégou et al., 2001; Tiunov and Dobrovolskaya, 2002). In addition, burrows may serve as a regeneration niche for plants in grassland ecosystems (Milcu et al., 2006).

The size and three-dimensional orientation of earthworm burrows has often been described by workers using non-destructive X-ray computed tomography (CT) (Joschko et al., 1991; Jégou et al., 1999; Bastardie et al., 2003). Such measurements are useful for evaluating the spatial pattern of earthworm burrows, which affects water infiltration in ecosystems, but earthworm burrows cannot be considered permanent structures in the soil profile. Francis et al. (2001) reported that *Aporrectodea caliginosa* created temporary burrows and filled 72–85% of them within 20 days, while *Lumbricus rubellus* burrows lasted longer (56–64% were filled between successive CT scans). In contrast, anecic earthworms like *Lumbricus terrestris* tend to intensively reuse their continuous, vertical burrows. Bastardie et al. (2005) extracted soil cores from a permanent pasture and found two burrow forms, very short, disconnected burrows with small diameters that were probably built by endogeic species like *A. caliginosa* and *Octolasion lacteum*, and long, continuous burrows with large diameters built by *L. terrestris* and *Nicodrilus giardi*. The volume of soil occupied by the two types of burrows varied temporally, and this was attributed to differences in burrowing activities and longevity of burrows created by the earthworm species at their study site (Bastardie et al., 2005). The burrow systems of earthworms are affected by site-specific factors such as soil texture and topography, as well as the types of earthworms present (Capowiez et al., 1998; Bastardie et al., 2005), but earthworm populations respond in predictable ways to fluctuations in soil temperature and moisture. Kretzschmar (1982) reported that the seasonal variation in burrow numbers and forms in a grassland was related to fluctuations in water content and temperature. Researchers wishing to understand the temporal dynamics of burrowing, to better estimate water and chemical transport through these macropores or to predict nutrient transformations and trophic relationships in the drilosphere, require detailed information on how earthworm burrowing fluctuates with changing soil temperature and moisture conditions.

The objective of this study was to determine how burrowing by *A. caliginosa* and *L. terrestris* were influenced by soil temperature and moisture, using laboratory microcosms.

Materials and methods

Collection of earthworms, soil and litter

Juvenile *Aporrectodea* spp. were collected by hand-sorting soil (0–15 cm depth), while juvenile *Lumbricus* spp. was extracted with 0.5% formalin and rinsed well with tap water. Adults collected from the same site were identified as *A. caliginosa* (Sav.), while the juvenile *Lumbricus* spp. were *L. terrestris* L. (Reynolds, 1977). Earthworms were placed in 37 L plastic containers with field-moist soil from the collection site, a fine, mixed, frigid Typic Endoaquent classified as a Chicot sandy-loam. This soil came from an agricultural field under soybean (*Glycine max* L. Merr.) production at the Macdonald Campus Farm of McGill University, Ste-Anne-de-Bellevue, Québec, Canada (45° 28′N, 73° 45′W). It contained 580 g kg^{-1} of sand, 300 g kg^{-1} of silt and 120 g kg^{-1} of clay with 24.5 g organic C kg^{-1}, 1.98 g total N kg^{-1} and pH (H_2O) of 5.9. Soil in the plastic containers was moistened to near field capacity and litter was added to provide sufficient food for earthworms, which were kept in these containers in the laboratory for about 6 weeks. The litter was ground (< 1 mm mesh) soybean stems and leaves collected at the pod stage, which contained 443 g organic C kg^{-1} and 40.9 g total N kg^{-1}, and ground (< 1 mm mesh) composted cattle manure containing 383 g organic C kg^{-1} and 19.9 g total N kg^{-1}. This soil and litter was also used in the experimental chambers.

Experimental chambers

The clear plexiglass chambers (45 cm high × 45 cm wide) used in this study allowed easy monitoring of earthworm casting and burrowing activities. For a description of the chamber dimensions and construction, the reader is referred to Whalen et al. (2004). Briefly, the chambers were prepared by placing 3 cm of cardboard at the bottom for support, and inserting a 5-cm-wide strip of plexiglass along each side, so the chamber was enclosed on the bottom and two sides. The thickness of the bottom and side panels was 3 mm in chambers housing *A. caliginosa* and 4.5 mm in

chambers prepared for *L. terrestris*. We then placed 19 cm of pre-moistened soil in the bottom of the chamber and covered it with 19 cm of pre-moistened soil plus litter (6.5 g compost and 4.5 g ground soybean kg^{-1} soil). The area covered by soil and soil/litter mixture in the chambers was 0.14 m^2, and the soil bulk density was approximately 1.0 g cm^{-3}. There was a 4-cm gap between the soil surface and the top of the chamber. Chambers were then incubated in the dark at 20 °C for 1 week before adding the earthworms.

Experimental design

The experiment was designed as a completely randomized factorial design with four temperatures (5, 10, 15 and 20 °C), and two soil moisture levels (25% and 30% gravimetric moisture content), for a total of eight factorial treatments. There were five replicates of each treatment. The experimental unit (replicate) was the plexiglass chamber described above, and each chamber housed a single earthworm.

Since matric potential is a more meaningful way to express biological water availability than % water content, we converted the gravimetric moisture content to matric potential using the Rosetta software programme (Schaap, 2000), adjusting for texture and bulk density using the van Genuchten function for water retention (van Genuchten, 1980; Schaap et al., 1998). The calculated matric potentials ($\pm$standard deviation) were -5 ± 1 and -11 ± 2 kPa, corresponding to 30% and 25% gravimetric moisture content, respectively.

Prior to their introduction to the chambers, earthworms were placed in plastic jars on damp paper towels to void their guts for 24 h, then patted dry and weighed (gut free fresh weight). The average ($\pm$standard error) mass of *A. caliginosa* was 0.50 ± 0.01 g fresh weight ($n = 40$) while *L. terrestris* weighed 1.81 ± 0.03 g fresh weight ($n = 40$). A single earthworm was placed on the soil surface in each chamber, and the chambers were placed in one of four Conviron incubators set at 5, 10, 15 or 20 °C. When earthworms are placed in laboratory chambers containing sieved, unstructured soil, they spend the first 2–3 days constructing burrows, leading to an elevated rate of surface casting (Bolton and Phillipson, 1976; Scheu, 1987). Therefore, measurement of surface casting and burrowing started on the fourth day after adding the earthworm, and these activities were measured every 24 h from day 4 to day 7 of the study. New surface casts and burrows were marked distinctly with colored markers every day. The outlines of surface casts were traced on transparent acetate sheets, which were then scanned and the total surface cast area (cm^2) was calculated using the software Winrhizo Pro 5.0a (Regent Instruments Inc., Ste-Foy, Québec, Canada). Total burrow length (cm) was calculated by running a string along the newly marked burrows each day, measuring the length of string, and summing the daily measurements. The maximum burrow depth (cm) was the distance from the soil surface to the bottom of the deepest burrow observed in the chamber. At the end of the 4-day monitoring period, earthworms were taken out of the chambers and weighed after voiding their gut for 24 h.

Statistical analysis

Earthworm surface casting data were log transformed (log +1) to adjust for normality and equalize variance before analysis. The effects of soil temperature and moisture, and the temperature-moisture interaction, on earthworm parameters (change in mass, surface casting, burrow length and maximum burrow depth) were evaluated using a two-factor analysis of variance (ANOVA) with the PROC GLM function of SAS (SAS System 9.1, SAS Institute Inc., Cary, NC).

Results

Mortality and changes in earthworm mass

Earthworm mortality was low, with no mortality of *A. caliginosa* and 5% mortality for *L. terrestris*. Upon removal from the plexiglass chambers, earthworm mass averaged 0.53 ± 0.02 g fresh weight ($n = 40$) for *A. caliginosa* and 1.99 ± 0.04 g fresh weight ($n = 38$) for *L. terrestris*. In incubators at 5 and 10 °C, *A. caliginosa* tended to lose weight, as did *L. terrestris* at 5 °C (Tables 1 and 2). *A. caliginosa* gained weight when they were kept at 15 and 20 °C, while the greatest weight gain by *L. terrestris* was recorded at 20 °C in soil moistened to -5 kPa (Tables 1 and 2).

Temperature and moisture effects on surface casting and burrowing activities

Temperature, soil moisture and the interaction between temperature and moisture were all significant factors affecting surface casting and burrowing activity (Tables 1 and 2). In general, surface casting and burrowing activity increased with increasing temperature. More surface casting

Table 1. Temperature and soil moisture effects on the surface casting and burrowing activity of juvenile *A. caliginosa*.

Temperature (ºC)	Soil matric potential (kPa)	Change in mass (g fresh weight)	Surface cast area (cm^2)	Burrow length (cm)	Maximum burrow depth (cm)
5	−11	−0.05±0.02	0.10±0.09	8.9±2	11±2
10	−11	−0.02±0.01	2.4±0.6	22±3	15±1
15	−11	0.08±0.03	2.5±1.0	48±10	21±2
20	−11	0.11±0.03	2.3±0.4	82±9	23±3
5	−5	0.01±0.02	5.4±0.8	11±2	8.2±1
10	−5	−0.02±0.03	11±1.6	25±2	9.6±2
15	−5	0.12±0.04	9.0±1.1	28±6	8.7±2
20	−5	0.06±0.02	11±1.4	33±2	15±5
Temperature		$P = 0.0001$	$P = 0.0007$	$P = 0.0001$	$P = 0.0032$
Moisture		NS	$P = 0.0001$	$P = 0.0002$	$P = 0.0004$
Temperature × moisture		NS	NS	$P = 0.0001$	NS

Values are the mean±standard error. Significance of treatment effects was determined by ANOVA, NS = not significant ($P > 0.10$).

Table 2. . Temperature and soil moisture effects on the surface casting and burrowing activity of juvenile *L. terrestris*.

Temperature (°C)	Soil matric potential (kPa)	Change in mass (g fresh weight)	Surface cast area (cm^2)	Burrow length (cm)	Maximum burrow depth (cm)
5	−11	−0.13±0.04	3.5±0.8	20±7	16±1
10	−11	0.11±0.03	6.0±1.5	48±8	20±1
15	−11	0.06±0.02	3.7±1.0	70±19	21±1
20	−11	0.26±0.08	2.9±1.1	121±25	28±4
5	−5	0.08±0.03	2.1±0.6	1.4±0.7	4.5±1
10	−5	0.25±0.08	9.2±2.0	15±4	17± 4
15	−5	0.40±0.13	14±1.4	30±7	24±2
20	−5	0.41±0.13	19±2.2	37±3	22±3
Temperature		$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$
Moisture		$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0238$
Temperature × moisture		NS	$P = 0.0001$	$P = 0.0646$	$P = 0.0806$

Values are the mean±standard error. Significance of treatment effects was determined by ANOVA, NS = not significant ($P > 0.10$).

was observed when *A. caliginosa* and *L. terrestris* were placed in soil at −5 kPa than −11 kPa, but the burrows were longer in soil at −11 kPa than −5 kPa (Tables 1 and 2). The maximum depth of burrows created by *A. caliginosa* ranged from 8.2 to 23 cm, and burrow depth increased as the temperature increased (Table 1). The shallowest burrow (4.5 cm) was created by *L. terrestris* housed in chambers at 5 °C with soil at −5kPa, but their burrows typically ranged in depth from 16 to 28 cm, increasing as the temperature increased (Table 2).

Discussion

The plexiglass chambers were quite useful in monitoring the surface casting and burrowing activities of *A. caliginosa* and *L. terrestris*. There was little mortality of earthworms housed in these chambers, and many treatments led to weight gain by earthworms, particularly when the soil temperature was 15 or 20 °C. This is consistent with the increase in growth rates with increasing soil temperatures reported for *Aporrectodea rosea*, *Aporrectodea tuberculata* and *L. terrestris* (Bolton and Phillipson, 1976; Berry and Jordan, 2001; Wever et al., 2001). Earthworms often lose weight or enter diapause when soils are too dry (Booth et al., 2000; Holmstrup, 2001). Eriksen-Hamel and Whalen (2006) reported that growth rates of *A. caliginosa* were greatest at soil water potentials of −5 and −11 kPa, suggesting that these matric potentials would favour earthworm weight gain and activity, as we observed in this study.

Higher temperatures and soil moisture levels were also favourable for surface casting. Surface cast production typically increases as the soil temperature increases, due to greater consumption of soil and organic substrates (Bolton and Phillipson, 1976; Scheu, 1987; Daniel, 1991). Greater surface casting in wet soils than dry soils has been reported for other lumbricid earthworms (Hindell et al., 1994; Daniel et al., 1996). However, Zaller and Arnone (1999) reported no difference in surface casting in field plots that received ambient rainfall or ambient plus 280 mm rainfall $year^{-1}$, although soil moisture was consistently greater in the plots receiving additional rainfall. We did not quantify subsurface casting in this study, but our observations were similar to Whalen et al. (2004), who reported that subsurface casts were $<10\%$ of the total cast production by juvenile *Aporrectodea* spp. and *Lumbricus* spp. in these plexiglass chambers.

Although burrow length and maximum burrow depth increased with increasing temperature, there was less burrowing in wetter soil (−5 kPa) than drier soil (−11 kPa). In addition, *A. caliginosa* and *L. terrestris* deposited more casts at the surface of the wetter soil than the drier soil, suggesting that they consumed more soil and organic substrates under these conditions. Surface soil mixed with litter is a more palatable substrate when wetted, leading to intensive feeding and limited burrowing by lumbricid earthworms (Martin, 1982). *L. terrestris* gained more weight at −5 kPa than at −11 kPa, which is consistent with ingesting more soil and N-rich litter (Shipitalo et al., 1988). Although *A. caliginosa* and other earthworms create burrows by ingesting and removing the soil in their path, particularly in compacted soils (Dexter, 1978; Kretzschmar, 1991), they generate sufficient axial and radial pressure to push aside soil particles in non-compacted soils (McKenzie and Dexter, 1988a, b). We suggest that conditions in the drier soil were more conducive to this type of tunnelling and permitted earthworms to explore a larger volume of soil, deeper in the chamber. At 20 °C, the burrow length created by earthworms at −11kPa was 2.5–3.3 times the burrow length generated in the wetter soil (−5 kPa), and the maximum burrow depth was 6–8 cm deeper.

In the field, *A. caliginosa* and *A. rosea* generate mostly horizontal burrows with a mean length of 39.2 cm, not exceeding 25 cm in depth (McKenzie and Dexter, 1993). Lavelle (1997) found that *A. rosea* creates burrows mostly in the 0–20 cm depth, although deep vertical burrows extending to 80 cm are built when soils become very dry, as this species retreats deep in the soil during diapause. These results are consistent with the burrowing depth reported for *A. caliginosa* in this study. Francis et al. (2001) packed large cylinders (24.1 cm diameter) with topsoil and subsoil to a depth of 50 cm, and found that most burrows created by *A. caliginosa* were in the top 10 cm. These burrows were temporary, since 72–85% were filled with soil in the 20-day interval between successive CT scans. We did not observe backfilling of burrows during the short duration of this study.

In contrast, *L. terrestris* generally produces a single, semi-permanent vertical burrow. In the field, their burrows can extend to 1 m (Shipitalo and Butt, 1999; Nuutinen and Butt, 2003), but the maximum burrow depth in laboratory studies is generally limited by the size of the core or microcosm used (Bastardie et al., 2003). The plexiglass chamber was not deep enough, nor wide enough, to permit deep burrowing and midden building by *L. terrestris*. All of the litter was mixed with soil in the top 19 cm of the chamber, and generally *L. terrestris* confined their burrowing activities to this upper layer, not venturing below 28 cm in the chamber. When soil conditions were the most unfavourable (cold and wet), *L. terrestris* built a burrow large enough for its body, curled up and remained virtually inactive for the duration of the study.

Our study confirms that soil temperature and moisture strongly influence earthworm burrowing activities. Weight gain and surface casting by juveniles of *A. caliginosa* and *L. terrestris* were greatest at 20 °C and a water potential of −5 kPa, but burrowing was favoured more in drier soil (−11 kPa). Higher temperatures were not tested since the survival of many lumbricid species decreases above 20 °C (Edwards and Bohlen, 1996). Our results suggest more intensive feeding and limited burrowing in wetter soil, while slightly drier, non-compacted soil may permit more tunnelling and exploration in the soil profile by earthworms. How these burrowing activities affect soil microbial and microfaunal communities is not fully known. A priming effect (sensu Brown et al., 2000) is expected when earthworms ingest soil and litter, and then deposit them in casts at the soil surface or within abandoned burrows. As earthworms move through the soil, they secrete mucus to facilitate their movement, which can stimulate microbial activity in the drilosphere (Brown et al., 2000). The influence of burrowing activities on the soil foodweb organisms warrants further investigation.

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References

Bastardie, F., Capowiez, Y., de Dreuzy, J.-R., Cluzeau, D., 2003. X-ray tomographic and hydraulic characterization of burrowing by three earthworm species in repacked soil cores. Appl. Soil Ecol. 24, 3–16.

Bastardie, F., Capowiez, Y., Cluzeau, D., 2005. 3D characterisation of earthworm burrow systems in natural soil cores collected from a 12-year-old pasture. Appl. Soil Ecol. 30, 34–46.

Berry, E.C., Jordan, D., 2001. Temperature and soil moisture content effects on the growth of *Lumbricus terrestris* (Oligochaeta:Lumbricidae) under laboratory conditions. Soil Biol. Biochem. 33, 133–136.

Bolton, P.J., Phillipson, J., 1976. Burrowing, feeding, egestion and energy budgets of *Allolobophora rosea* (Savigny) (Lumbricidae). Oecologia 23, 225–245.

Booth, L.H., Heppelthwaite, V., McGlinchy, A., 2000. The effect of environmental parameters on growth, cholinesterase activity and glutathione *S*-transferase activity in the earthworm (*Aporrectodea caliginosa*). Biomarkers 5, 46–55.

Brown, G.G., Barois, I., Lavelle, P., 2000. Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains. Eur. J. Soil Biol. 36, 177–198.

Capowiez, Y., Pierret, A., Daniel, O., Monestiez, P., Kretzschmar, A., 1998. 3D skeleton reconstructions of natural earthworm burrow systems using CAT scan images of soil cores. Biol. Fertil. Soils 27, 51–59.

Daniel, O., 1991. Leaf-litter consumption and assimilation by juveniles of *Lumbricus terrestris* L. (Oligochaeta, Lumbricidae) under different environmental conditions. Biol. Fertil. Soils. 12, 202–208.

Daniel, O., Kohli, L., Schuler, B., Zeyer, J., 1996. Surface cast production by the earthworm *Aporrectodea nocturna* in a pre-alpine meadow in Switzerland. Biol. Fertil. Soils 22, 171–178.

Dexter, A.R., 1978. Tunnelling in soil by earthworms. Soil Biol. Biochem. 10, 447–449.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms, third ed. Chapman & Hall, London.

Edwards, W.M., Shipitalo, M.J., Owens, L.B., Dick, W.A., 1993. Factors affecting preferential flow of water and atrazine through earthworm burrows under continuous no-till corn. J. Environ. Qual. 22, 453–457.

Eriksen-Hamel, N.S., Whalen, J.K., 2006. Growth rates of *Aporrectodea caliginosa* (Oligochaeta: Lumbricidae) as influenced by soil temperature and moisture in disturbed and undisturbed soil columns. Pedobiologia 50, 207–215.

Francis, G.S., Tabley, F.J., Butler, R.C., Fraser, P.M., 2001. The burrowing characteristics of three common earthworm species. Aust. J. Soil Res. 39, 1453–1465.

Gorres, J.H., Savin, M.C., Amador, J.A., 1997. Dynamics of carbon and nitrogen mineralization, microbial biomass, and nematode abundance within and outside the burrow walls of anecic earthworms (*Lumbricus terrestris*). Soil Sci. 162, 666–671.

Hindell, R.P., McKenzie, B.M., Tisdal, J.M., Silvapulle, M.J., 1994. Relationships between casts of geophagous earthworms (*Lumbricidae, Oligochaeta*) and matric potential. Biol. Fertil. Soils 18, 119–126.

Holmstrup, M., 2001. Sensitivity of life history parameters in the earthworm *Aporrectodea caliginosa* to small changes in soil water potential. Soil Biol. Biochem. 33, 1217–1223.

Jégou, D., Hallaire, V., Cluzeau, D., Tréhen, P., 1999. Characterization of the burrow system of the earthworm *Lumbricus terrestris* and *Aporrectodea giardi* using X-ray computer tomography and image analysis. Biol. Fertil. Soils 29, 314–318.

Jégou, D., Schrader, S., Diestel, H., Cluzeau, D., 2001. Morphological, physical and biochemical characteristics of burrow walls formed by earthworms. Appl. Soil Ecol. 17, 165–174.

Joschko, M., Graff, O., Muller, P.C., Kotzke, K., Lindner, P., Pretschner, D.P., Larink, O., 1991. A non-destructive method for the morphological assessment of earthworm burrow system in three dimensions by X-ray computer tomography. Biol. Fertil. Soils 11, 88–92.

Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil Till. Res. 61, 61–76.

Kretzschmar, A., 1982. The burrow system of earthworms in grassland – seasonal variations of field observations. Rev. Ecol. Biol. Sol 19, 579–591.

Kretzschmar, A., 1991. Burrowing ability of the earthworm *Aporrectodea longa* limited by soil compaction and water potential. Biol. Fertil. Soils 11, 48–51.

Langmaack, M., Schrader, S., Rapp-Bernhardt, U., Kotzke, K., 2002. Soil structure rehabilitation of arable soil degraded by compaction. Geoderma 105, 141–152.

Lavelle, C., 1997. Burrowing activity of *Aporrectodea rosea*. Pedobiologia 42, 97–101.

Martin, N.A., 1982. The interaction between organic matter in soil and the burrowing activity of three species of earthworms (Oligochaeta, Lumbricidae). Pedobiologia 24, 185–190.

McKenzie, B.M., Dexter, A.R., 1988a. Axial pressures generated by the earthworm *Aporrectodea rosea*. Biol. Fertil. Soils 5, 323–327.

McKenzie, B.M., Dexter, A.R., 1988b. Radial pressures generated by the earthworm *Aporrectodea rosea*. Biol. Fertil. Soils 5, 328–332.

McKenzie, B.M., Dexter, A.R., 1993. Size and orientation of burrows made by the earthworms *Aporrectodea rosea* and *A. caliginosa*. Geoderma 56, 233–241.

Milcu, A., Schumacher, J., Scheu, S., 2006. Earthworms (*Lumbricus terrestris*) affect plant seedling recruitment and microhabitat heterogeneity. Funct. Ecol. 20, 261–268.

Nuutinen, V., Butt, K.R., 2003. Interaction of *Lumbricus terrestris* L. burrows with field subdrains. Pedobiologia 47, 578–581.

Reynolds, J.W., 1977. The Earthworms (Lumbricidae and Sparganophilidae) of Ontario. Life Sci. Misc. Publishers, Royal Ontario Museum, Toronto.

Schaap, M.G., 2000. Rosetta, version 1.2. US Salinity Laboratory, ARS-USDA, Riverside, CA, USA, 〈www.ussl.ars.usda.gov/models/rosetta/rosetta.htm〉.

Schaap, M.G., Leij, F.A., van Genuchten, M.T., 1998. Neural network analysis for hierarchical prediction of soil water retention and saturated hydraulic conductivity. Soil Sci. Soc. Am. J. 62, 847–855.

Scheu, S., 1987. The role of substrate feeding earthworms (Lumbricidae) for bioturbation in a beechwood soil. Oecologia 72, 192–196.

Shipitalo, M.J., Butt, K.R., 1999. Occupancy and geometrical properties of *Lumbricus terrestris* L. burrows affecting infiltration. Pedobiologia 43, 782–794.

Shipitalo, M.J., Protz, R., Tomlin, A.D., 1988. Effect of diet on the feeding and casting activity of *Lumbricus terrestris* and *L. rubellus* in laboratory culture. Soil Biol. Biochem. 20, 233–237.

Shuster, W.D., Shipitalo, M.J., Subler, S., Aref, S., McCoy, E.L., 2003. Earthworm additions affect leachate production and nitrogen losses in typical Midwestern agroecosystems. J. Environ. Qual. 32, 2132–2139.

Tiunov, A.V., Scheu, S., 1999. Microbial respiration, biomass, biovolume and nutrient status in burrow walls of *Lumbricus terrestris* L. (Lumbricidae). Soil Biol. Biochem. 31, 2039–2048.

Tiunov, A.V., Dobrovolskaya, T.G., 2002. Fungal and bacterial communities in *Lumbricus terrestris* burrow walls: a laboratory experiment. Pedobiologia 46, 595–605.

van Genuchten, M.T., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Sci. Am. J. 44, 892–898.

Wever, L.A., Lysyk, T.J., Clapperton, M.J., 2001. The influence of soil moisture and temperature on the survival, aestivation, growth and development of juvenile *Aporrectodea tuberculata* (Eisen) (Lumbricidae). Pedobiologia 45, 121–133.

Whalen, J.K., Sampedro, L., Waheed, T., 2004. Quantifying surface and subsurface cast production by earthworms under controlled laboratory conditions. Biol. Fertil. Soils 39, 287–291.

Zaller, J.G., Arnone, J.A., 1999. Earthworm and soil moisture effects on the productivity and structure of grassland communities. Soil Biol. Biochem. 31, 517–523.