Available online at www.sciencedirect.com

Applied Soil Ecology 28 (2005) 15–22

Applied Soil Ecology

www.elsevier.com/locate/apsoil

Role of soil water content in the carbon and nitrogen dynamics of *Lumbricus terrestris* L. burrow soil

José A. Amador[a,*], Josef H. Görres[a], Mary C. Savin[b]

[a]*Laboratory of Soil Ecology and Microbiology, 024 Coastal Institute in Kingston,*
University of Rhode Island, Kingston, RI 02881, USA
[b]*Department of Crop, Soil, and Environmental Sciences, 115 Plant Science Building,*
University of Arkansas, Fayetteville, AR 72701, USA

Received 29 May 2002; accepted 14 June 2004

Abstract

We evaluated the role of soil water content in controlling C and N dynamics within the drilosphere created by the anecic earthworm *Lumbricus terrestris* (L.). Mesocosms (volume = 3.1 l) were each amended with corn litter and three earthworms. Control treatments received no earthworms and no other earthworm species were present in the soil. WET and DRY treatments received a total of 9.25 cm and 3.25 cm of water, respectively. Water was added on weeks 1, 3, 7, and 10 at a rate of 2.0 cm per mesocosm for WET treatments and 0.5 cm per mesocosm for DRY treatments. Mesocosms were sampled destructively after incubation at 18–20 °C for 0, 3, 7, and 13 weeks. The water content of WET burrow soil ranged from 0.12 g g^{-1} to 0.18 g g^{-1} and was significantly higher than in the DRY treatment throughout the incubation period. The live weight of earthworms was significantly higher in the WET treatment only on week 13, whereas litter consumption was significantly lower in the DRY treatment for week 13. Carbon mineralization, measured as CO_2 evolved after a 24-h incubation, was consistently higher in WET than in DRY burrow soil. Effects of differences in soil water content were also apparent for biomass C and metabolic quotient. Soil water content did no affect the total C concentration of burrow soil. DRY burrow soil had consistently lower levels of nitrate than WET soil throughout the experiment. Lower levels of ammonium and inorganic N were observed for WET burrow soil on weeks 3 and 7. Water content did not have a significant effect on burrow soil total N. We concluded that the water content of the drilosphere affects both C and N dynamics and can affect the speciation of inorganic N; yet, the effects of soil water content do not appear to result from differences in the feeding activities of anecic earthworms.

Keywords: *Lumbricus terrestris*; Soil moisture; Carbon dynamics; Nitrogen dynamics; Corn litter; Anecic earthworms

1. Introduction

Earthworms are thin-skinned annelids with little protection against moisture changes in the soil (Edwards and Bohlen, 1996). Water loss is an

---

* Corresponding author. Tel.: +1 401 874 2902;
fax: +1 401 874 4561.
E-mail address: jam7740u@postoffice.uri.edu (J.A. Amador).

0929-1393/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.apsoil.2004.06.009

important aspect of earthworm physiology and ecology (Turner, 2000), and they are generally more active in moist soils than dry ones (Edwards and Bohlen, 1996). Earthworm survival (Roots, 1956; Gunadi et al., 2003), growth (Dominguez and Edwards, 1997; Berry and Jordan, 2001), migration (Edwards and Bohlen, 1996), cocoon production (Parmelee and Crossley, 1988), food consumption (Daniel, 1991), and casting (Scheu, 1987) are affected by ambient soil moisture.

Soil water content regulates microbial processes and ecological interactions involved in nutrient cycling. It affects the rate and pathways for microbial transformations of nitrogen (Linn and Doran, 1984) and carbon (Amador and Jones, 1997; Skopp et al., 1990). The water content of soil also regulates grazing and predation by the soil microfauna, and associated nutrient transformations (Elliott et al., 1980; Görres et al., 1999; Savin et al., 2001).

The effects of anecic earthworms on biogeochemical transformations within the soil result from the interaction of various factors, including enhanced movement of gases and water within the soil profile via burrows (Devliegher and Verstraete, 1997), enrichment of burrows with detritus (Devliegher and Verstraete, 1995; Amador et al., 2003), the digestion and decomposition of detritus by earthworms (Devliegher and Verstraete, 1995), and the release of nutrients by the microfauna and microflora in the drilosphere (Görres et al., 1997; Parkin and Berry, 1999). The water content of soil can affect all of these factors directly or indirectly. Elucidation of the role of soil moisture in controlling C and N dynamics in earthworm burrows is thus an important aspect of understanding the role of earthworms in the biogeochemical cycling of C and N in soil.

Although the effects of soil water content on the activity of anecic earthworms are well-recognized, an evaluation of the impact of moisture regime on the effects of anecic earthworms on carbon and nutrient transformations in soil is lacking. Soil moisture is an integral part of crop production strategies that may impinge on the contribution of anecic earthworms to crop nutrition. We conducted an experiment to assess the effects of soil moisture on dynamics of C and N in the soil surrounding the burrows of the anecic earthworm *Lumbricus terrestris* (L.). Our objectives were to test the effects of soil water content on earthworm foraging activity and the specific biogeochemistry of C and N within burrows. We tested two hypotheses on the effects of moisture on burrow C and N dynamics: (1) they result from effects on earthworm activities (e.g. feeding on litter), and (2) they result from effects on biogeochemical transformations within the burrows.

2. Materials and methods

2.1. Soil

Soil was collected in November 1998 from the Ap and B horizons of an old field in the Peckham Farm Research Area of the University of Rhode Island, Kingston, RI. The soil at the site is an Enfield silt loam (coarse-silty over sandy or sandy-skeletal, mixed, active, mesic Typic Dystrudepts) with a soil organic matter content of 3.6%. The soil was sieved through a 5-mm-mesh metal screen.

2.2. Plant litter and earthworms

Senescent corn leaves were collected from a no-till, organic corn field at Casey Farm in Saunderstown, RI, in October 1998. Leaves were stored in the dark at 4 °C for approximately 4 months—by then, the leaves were partially decomposed, as determined by visual inspection. Leaves were cut into approximately 2-cm-long strips. The mean C content of the litter was 38%, with an N content of 1.8% and a C/N ratio of 21:1, determined using a Carlo Erba N/C analyzer (model NA 1500, series 2, Milan, Italy).

Adult earthworms (*L. terrestris* L.) were purchased from a commercial outlet in North Kingstown, RI, 1 day prior to the experiment and stored in the dark at 4 °C. The average initial live weight of the earthworms was determined based on a subsample of 24 individuals.

2.3. Mesocosms

Experimental mesocosms consisted of 10-cm-inner-diameter and 0.5-m-long white PVC cores filled with sieved soil to a depth of 40 cm (volume of soil = 3.1 l). The bottom and top of the core were fitted with a fine fiberglass mesh (held in place with a rubber band) to retain soil and prevent earthworm escape. Corn litter was placed on the surface of the soil to a depth of ~5 cm (9 g dry wt.); this amount of litter corresponded to an addition of 3.42 g C and 0.16 g N per mesocosm. In order to mimic field conditions, litter was not replenished during the course of the experiment. All mesocosms received 1.25 cm of water at the onset of the experiment to ensure sufficient initial soil moisture for earthworm survival.

The experiment consisted of four treatments: (1) earthworms present, wet conditions (WET); (2) control with earthworms absent, wet conditions (CTRL-WET); (3) earthworms present, dry conditions (DRY); and (4) control with earthworms absent, dry conditions (CTRL-DRY). Each treatment was replicated three times per sampling time, and mesocosms were randomly distributed and incubated in the laboratory at 18–20 °C. Three individuals of *L. terrestris* were added to each mesocosm in the WET and DRY treatments, representing an initial population density of 370 earthworms m^{-2}. Water was added on weeks 1, 3, 7, and 10 at a rate of 2.0 cm per mesocosm for WET treatments and 0.5 cm per mesocosm for DRY treatments. The total amount of water added to each mesocosm was 9.25 cm (WET) and 3.25 cm (DRY). These rates correspond to approximately one-third and one-ninth the average precipitation from April to June in Kingston, RI, respectively (NOAA, 1975).

2.4. Sampling

Each treatment was sampled destructively at 0, 3, 7, and 13 weeks. All the litter was removed from the soil surface, soil particles removed manually, the litter placed in a sealable plastic bag, and stored in the dark at 4 °C. We defined burrow soil as that within 5 mm of the macropore wall. Cores were divided into 10-cm sections and soil removed from all the burrow walls by excavation with a spatula. All loose plant residues found in the burrows were removed using tweezers, soil particles removed manually, placed in a sealable plastic bag, and stored in the dark at 4 °C. Burrow soil was kept separate, with soil from different depths pooled and placed in sealable plastic bags, and then stored at 4 °C. Soil was mixed thoroughly before subsampling.

Earthworms were placed in a tray with water for approximately 15 min to remove soil particles from their surface. They were removed from the water, dried by placing on a tray lined with paper towels for approximately 15 min, and their live weight recorded.

2.5. Carbon mineralization

Soil (~2 g wet wt.) was placed in a 20-ml glass serum bottle and the vial sealed with a rubber septum and an aluminum crimp collar. The headspace of the vials was sampled and analyzed for CO_2 after incubation in the dark at 20 °C for 24 h. A 500-μl sample of headspace gases was removed by displacement using an automated headspace sampler (model 7000, Tekmar, Mason, Ohio) and injected into a gas chromatograph (model 14A, Shimadzu, Columbia, Maryland).

2.6. Carbon and nitrogen pools

Microbial biomass C was determined using the fumigation–extraction method described by Vance et al. (1987) using a 10-g soil sample and an extractant volume of 20 ml. Extracts were passed through a Whatman No. 42 filter and the total C content of the filtrate was determined with a model 5000 Shimadzu Total Organic Carbon Analyzer. The total C content of soil and plant material was determined with a Carlo Erba N/C analyzer. Metabolic quotient (qCO_2) was calculated by dividing the rate of C mineralization by the microbial biomass C of soil samples.

Levels of NO_3^- and NH_4^+ in soil were determined by extracting 1 g soil with 10 ml of a 2N KCl solution, followed by filtration and determination of NO_3^- and NH_4^+ concentration in the filtrate by automated colorimetric analysis using an Alpkem Flow Solution VI (Alpkem Corp., College Station, Texas). The total N content of soil was determined using a Carlo Erba N/C analyzer.

2.7. Soil water content

The moisture content of soil and plant materials was determined gravimetrically by drying to a constant weight at 105 °C and 65 °C, respectively.

2.8. Data analyses

To account for the effects of wet or dry conditions on control soils without earthworms, values of nitrate, ammonium, inorganic N, microbial biomass C, C mineralization, $q\text{CO}_2$, and soil C for control soil from each treatment (CTRL-WET and CTRL-DRY) were subtracted from those treatments receiving earthworms (WET and DRY). The difference between earthworm and control treatment for each moisture regime represents the effects of moisture regime on earthworm-affected soil. The standard deviation of the difference, σ_Δ, was calculated using the equation

$$\sigma_\Delta = \sqrt{(\sigma_\mathrm{E})^2 + (\sigma_\mathrm{C})^2}$$

where σ_E and σ_C are the standard deviations of the mean for earthworm and control treatments, respectively. Differences were analyzed using Student's *t*-test ($\alpha = 0.05$).

3. Results

The moisture content of burrow soil was significantly higher in the WET than in the DRY treatment for the duration of the experiment (Fig. 1). Soil moisture in the WET treatment increased from 0.11 g g^{-1} to 0.18 g g^{-1} during the first 3 weeks of the experiment, declining steadily with incubation time to 0.10 g g^{-1} after 13 weeks. In the DRY treatment, burrow soil moisture remained constant for the first 3 weeks, subsequently declining at a constant rate to a value of 0.04 g g^{-1} by week 13. We did not observe significant differences in water content between burrow and control soil for either moisture regime (data not shown).

Earthworm live weight remained constant in both treatments for the first 3 weeks of the experiment and declined at a constant rate over 7 and 13 weeks (Fig. 1). Differences in live weight were observed only on week 13, when it was significantly lower in the DRY than the WET treatment.

The time course of litter disappearance from the soil surface was similar in both treatments (Fig. 1), with the rate of litter loss declining with incubation time. The amount of litter remaining on the surface was slightly higher in the DRY than the WET treatment on weeks 3 and 7, and significantly higher on week 13, when values were 3.2 ± 0.4 g litter per mesocosm and 1.4 ± 0.2 g litter per mesocosm for DRY and WET treatments, respectively. In contrast, the amount of litter remaining in burrows was significantly higher in WET than in DRY treatments on weeks 3 and 7, with differences disappearing on week 13 (Fig. 1).

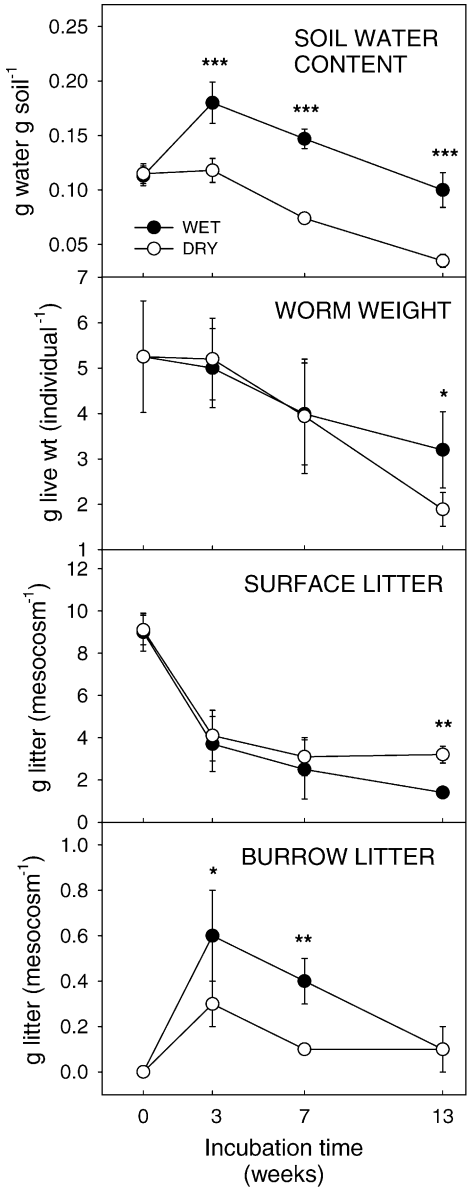

Fig. 1. Effects of WET and DRY treatments on earthworm burrow soil moisture, earthworm live weight, and amount of surface and burrow litter as a function of time. Bars represent one standard deviation (n = 3). $^{***}P < 0.001$; $^{**}P < 0.05$; $^{*}P < 0.10$.

Differences in C mineralization rate between treatments were apparent throughout the course of the experiment (Fig. 2). Rates of mineralization in burrow soil from WET and DRY treatments were higher than in their respective control soils, as indicated by positive differences (Δ). C mineralization was consistently lower in DRY than in WET burrow soil, with differences exhibiting a greater degree of statistical significance later in the experiment. Negative Δ values for burrow microbial biomass C were observed on most sampling dates for both WET

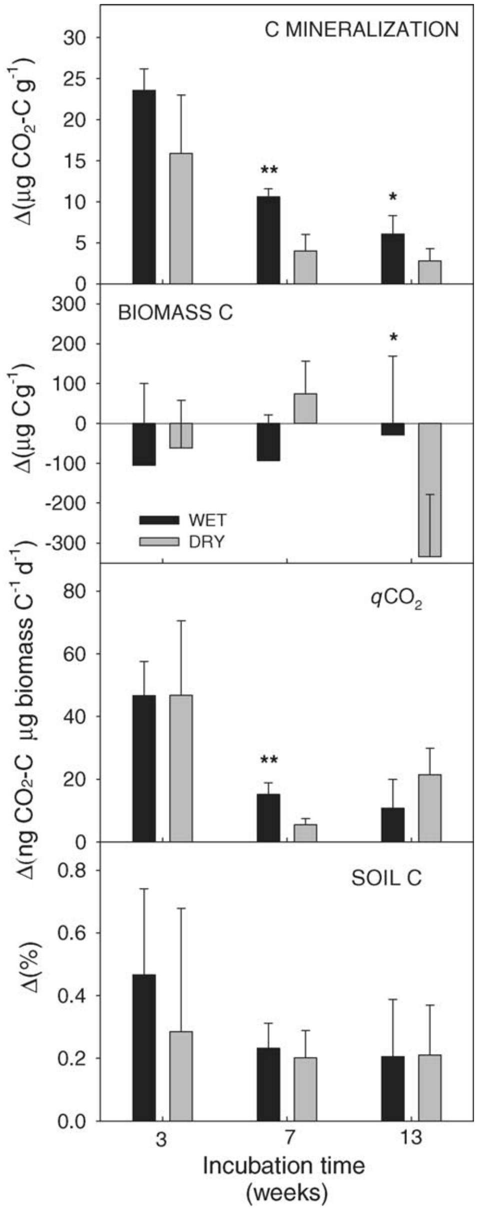

Fig. 2. Effects of WET and DRY treatments on C mineralization, microbial biomass C, $q\mathrm{CO_2}$, and soil C in burrow soil after incubation for 3, 7, and 13 weeks. Δ values represent the difference between earthworm and control treatments for each moisture regime. Bars represent one standard deviation ($n = 3$). $^{***}P < 0.001$; $^{**}P < 0.05$; $^{*}P < 0.10$.

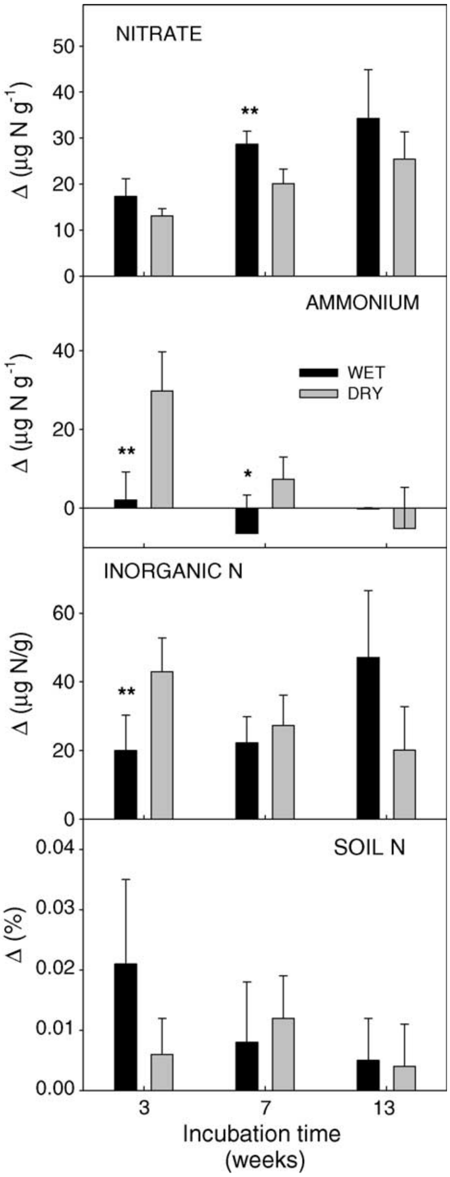

Fig. 3. Effects of WET and DRY treatments on levels of nitrate, ammonium, inorganic N, and soil N in burrow soil after incubation for 3, 7, and 13 weeks. Δ values represent the difference between earthworm and control treatments for each moisture regime. Bars represent one standard deviation ($n = 3$). $^{***}P < 0.001$; $^{**}P < 0.05$; $^{*}P < 0.10$.

and DRY treatments, indicating that it was lower than in control soil. No differences in biomass C between moisture regimes were apparent on week 3. However, differences between moisture treatments became more marked with incubation time, with higher biomass C in the DRY treatment on week 7, but lower values on week 13, than in the WET treatment. A high statistically significant difference in $q\mathrm{CO}_2$ was observed only on week 7, when $q\mathrm{CO}_2$ was higher in WET burrow soil (Fig. 2). Soil C was higher in burrow than in control soil for both DRY and WET treatments, and no differences in soil C were observed between moisture treatments (Fig. 2).

The WET treatment exhibited higher levels of nitrate in burrow soil throughout the course of the experiment (Fig. 3), with the strongest treatment differences on week 7. By contrast, lower levels of ammonium were found in the WET treatment burrow soil on weeks 3 and 7, with treatment differences disappearing by week 13 (Fig. 3). Levels of inorganic N in burrow soil were higher in the DRY treatment on week 3, but by week 13, inorganic N levels were higher in the WET treatment (Fig. 3). Burrow soil N was markedly higher in the WET treatment only for week 3 (Fig. 3).

4. Discussion

Moisture affected litter consumption by *L. terrestris* and live earthworm weight only after incubation for 13 weeks (Fig. 1). We observed significant differences between WET and DRY treatments in terms of soil moisture and both carbon and nitrogen variables on weeks 3 and 7 of the experiment, when no differences were observed in litter consumption or worm weight between moisture treatments (Figs. 2 and 3). These results contradict the hypothesis that moisture status regulated C and N transformations through its effects on earthworm activities. However, other activities carried out by earthworms may have been affected by moisture status. Exudate production could have differed under WET and DRY soil moisture regimes. Because exudates have high concentrations of organic N (Edwards and Bohlen, 1996; Scheu, 1991), differences in their production may explain differences in C and N dynamics between moisture treatments. There are few realistic estimates of urine or mucus excretion by earthworms (Parmelee et al., 1998). Because differences in exudate production were not measured in the present study, we cannot rule them out completely as an explanation for our results. However, the absence of statistically significant differences between soil moisture treatments in earthworm live weight (Fig. 1) and burrow soil C (Fig. 2) and N (Fig. 3) on weeks 3 and 7 tends to exclude differential exudate production as an explanation.

Our results support the hypothesis that moisture status affects C and N dynamics by its influence on biogeochemical transformations within the burrow. The positive response of C mineralization to increased moisture indicates that this process is limited by either water availability and/or physical factors associated with the connectivity of water-filled pores in the burrow. In most soils, carbon mineralization increases with increasing soil moisture content until saturation is reached (e.g. Linn and Doran, 1984; Skopp et al., 1990; Amador and Jones, 1997). Water may enhance C mineralization and stimulate microbial activity by acting as a solvent for organic substrates derived from litter and/or worm exudates. Higher moisture content allows these substances to diffuse within a greater proportion of the soil pore volume, making them more available to microorganisms. Greater connectivity of pore spaces may also benefit microbivorous fauna by increasing their access to microbial habitat. Microbivory is linked to enhanced C and N mineralization rates (Hassink et al., 1993; Marinissen and deRuiter, 1993). In a companion study to ours, Savin et al. (2004) found greater numbers of protozoa and of bacterivorous nematodes in *L. terrestris* drilosphere soil than in control treatments under a soil moisture regime equivalent to our WET treatment. Görres et al. (1997) have suggested that high values of $q\mathrm{CO}_2$ in anecic earthworm burrows result from grazing of microflora by nematodes. Higher values of $q\mathrm{CO}_2$ observed in the WET treatment on week 7 (Fig. 2) tend to support enhanced microbivory as one interpretation for our results. Alternatively, Tiunov and Scheu (1999) have suggested that elevated $q\mathrm{CO}_2$ values in burrow soil reflect adaptation of the microbial community to continuous resource additions by earthworm faeces and mucus.

Burrow moisture exerted a strong control on both the concentration and speciation of inorganic N. The

DRY treatment had higher levels of inorganic N early in the experiment, and this pool was composed primarily of ammonium (Fig. 3). By contrast, higher nitrate levels in burrow soil were associated with the WET soil water status, with little or no ammonium found in the soil in this treatment (Fig. 3). These data suggest that nitrification in earthworm burrow soil is limited by soil moisture. Ammonification in soil is less sensitive to water content than nitrification (Paul and Clark, 1996). The differential effects of soil water content on N transformations could result from low pore connectivity. Drury et al. (1991) have shown that ammonification and nitrification show a high degree of spatial separation. In highly connected, water-filled pore networks, ammonium can diffuse more readily from ammonification to nitrification sites, thus increasing the rate of nitrate production. This interpretation is consistent with the fact that both ammonium and nitrate were found in DRY treatment burrows, but very little ammonium was found in WET treatment burrows.

5. Conclusions

The relationship between soil water content and biogeochemical processes in drilosphere soil has potential implications for the fate of C and nutrients. Soil moisture values were within those observed under field conditions between March and June in this area (Görres et al., 1998), suggesting that these effects could be observed under field conditions. Furthermore, they occurred within weeks of burrow formation, indicating that they may be important at time scales relevant to C and nutrient transformations during periods of crop production. By controlling gaseous loses of C via mineralization, soil moisture may affect the extent to which C can accumulate in burrow soil, altering the effects of anecic earthworms on C storage and soil structure. Wet conditions promoted nitrate accumulation, whereas dry conditions promoted accumulation of ammonium, particularly within the first 7 weeks after burrow formation. Because nitrate is more mobile, higher concentrations of nitrate in burrows may cause losses due to diffusion into adjacent soil and/or leaching. Although not measured, denitrification probably was not a significant sink for nitrate at the moisture contents used in the present study (Parkin and Berry, 1999). Under drier conditions, nitrate diffusion and leaching are less likely, which could enhance conservation of inorganic N.

Acknowledgements

We thank the University of Rhode Island Facilities and Maintenance crew and Cheryl Tefft for help with obtaining and transporting soil, and Elizabeth Downing and Casey Farm for providing corn litter. Technical help from Wilfrid Rodriguez and Erika Nicosia is gratefully acknowledged. This study was funded by a grant from the USDA National Research Initiative Competitive Grants Program, the Rhode Island Agricultural Experiment Station, the University of Rhode Island's Partnership for the Coastal Environment, and personal funds of the authors.

References

Amador, J.A., Görres, J.H., Savin, M.C., 2003. Carbon and nitrogen dynamics in *Lumbricus terrestris* (L.) burrow soil: relationship to plant residues and macropores. Soil Sci. Soc. Am. J. 67, 1755–1762.

Amador, J.A., Jones, R.D., 1997. Response of carbon mineralization to combined changes in soil moisture and carbon–phosphorus ratio in a low-phosphorus Histosol. Soil Sci. 162, 275–282.

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.

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.

Devliegher, W., Verstraete, W., 1995. *Lumbricus terrestris* in a soil core experiment: nutrient-enrichment processes (NEP) and gut-associated processes (GAP) and their effect on microbial biomass and microbial activity. Soil Biol. Biochem. 27, 1573–1580.

Devliegher, W., Verstraete, W., 1997. Microorganisms and soil physico-chemical conditions in the drilosphere of *Lumbricus terrestris*. Soil Biol. Biochem. 29, 1721–1729.

Dominguez, J., Edwards, C.A., 1997. Effects of stocking rate and moisture content on the growth and maturation of *Eisenia andrei* (Oligochaeta) in pig manure. Soil Biol. Biochem. 29, 743–746.

Drury, C.F., Voroney, R.P., Beauchamp, E.G., 1991. Availability of NH_4^+ to microorganisms and the soil internal cycle. Soil Biol. Biochem. 23, 165–169.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms, third ed. Chapman & Hall, London, 426 pp.

Elliott, E.T., Anderson, R.V., Coleman, D.C., Cole, C.V., 1980. Habitable pore space and microbial trophic interactions. Oikos 35, 327–335.

Görres, 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. 62, 666–671.

Görres, J.H., DiChiaro, M.J., Lyons, J.B., Amador, J.A., 1998. Spatial and temporal patterns of soil biological activity in a forest and an old field. Soil Biol. Biochem. 30, 219–230.

Görres, J.H., Savin, M.C., Neher, D.H., Weicht, T.R., Amador, J.A., 1999. Grazing in a porous environment: I. The effect of pore structure on C and N mineralization. Plant Soil 212, 75–83.

Gunadi, B., Edwards, C.A., Blount, C., 2003. The influence of different moisture levels on the growth, fecundity and survival of *Eisenia fetida* (Savigny) in cattle and pig manure solids. Eur. J. Soil Biol. 39, 19–24.

Hassink, J., Bowman, L., Zwart, K.B., Brussaard, L., 1993. Relationship between habitable pore space, soil biota and mineralization rates in grassland soils. Soil Biol. Biochem. 25, 47–55.

Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. Soil Sci. Soc. Am. J. 48, 1267–1272.

Marinissen, J.Y.C., deRuiter, P.C., 1993. Contribution of earthworms to carbon and nitrogen cycling in agro-ecosystems. Agric. Ecosyst. Environ. 47, 59–74.

NOAA, 1975. Climatography of the United States No. 20. Climate of Kingston, RI Department of Commerce, National Climatic Center, Asheville, NC.

Parkin, T.B., Berry, E.C., 1999. Microbial nitrogen transformations in earthworm burrows. Soil Biol. Biochem. 31, 1765–1771.

Parmelee, R.W., Bohlen, P.J., Blair, J.M., 1998. Earthworms and nutrient cycling processes: integrating across the ecological hierarchy. In: Edwards, C.A. (Ed.), Earthworm Ecology, CRC Press, Boca Raton, FL, pp. 123–143.

Parmelee, R.W., Crossley Jr., D.A., 1988. Earthworm production and role in the nitrogen cycle of a no-tillage agroecosystem on the Georgia piedmont. Pedobiologia 32, 351–361.

Paul, E.A., Clark, F.E., 1996. Soil Microbiology and Biochemistry, second ed. Academic Press, San Diego, CA, 340 pp.

Roots, B.I., 1956. The water relations of earthworms. II. Resistance to desiccation and immersion, and behaviour when submerged and when allowed a choice of environment. J. Exp. Biol. 33, 29–44.

Savin, M.C., Görres, J.H., Neher, D.A., Amador, J.A., 2001. Biogeophysical factors influencing soil respiration and mineral nitrogen content in an old field soil. Soil Biol. Biochem. 33, 429–438.

Savin, M.C., Görres, J.H., Amador, J.A., 2004. Microbial and microfaunal community dynamics in artificial and *Lumbricus terrestris* (L.) burrows. Soil Sci. Soc. Am. J. 68, 116–124.

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

Scheu, S., 1991. Mucus excretion and carbon turnover of endogeic earthworms. Biol. Fertil. Soils 5, 217–220.

Skopp, J., Dawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil water content. Soil Sci. Soc. Am. J. 54, 1619–1625.

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, 2031–2048.

Turner, J.S., 2000. The Extended Organism, Harvard University Press, Cambridge, MA, 235 pp.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.