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# Grazing in a porous environment: 1. The effect of soil pore structure on C and N mineralization

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**Abstract**

The porous soil environment constrains grazing of microorganisms by microbivorous nematodes. In particular, at matric potentials at which water-filled pore spaces have capillary diameters less than nematode body diameters the effect of grazing, e.g. enhanced mineralization, should be reduced ('*exclusion hypothesis*') because nematodes cannot access their microbial forage. We examined C and N mineralization, microbial biomass C (by fumigation-extraction), the metabolic quotient (C mineralization per unit biomass C), nematode abundance, and soil water content in intact soil cores from an old field as a function of soil matric potential ($-3$ to $-50$ kPa). We expected, in accordance with the *exclusion hypothesis*, that nematode abundance, N and C mineralization would be reduced as matric potential decreased, i.e. as soils became drier. N mineralization was significantly greater than zero for $-3$ kPa but not for $-10$, $-20$ and $-50$ kPa. Microbial biomass C was less at $-50$ kPa than at $-10$ kPa, but not significantly different from biomass C at $-3$ and $-20$ kPa. The metabolic quotient was greatest at $-50$ kPa than any of the other matric potentials. From the *exclusion hypothesis* we expected significantly fewer nematodes to be present at $-50$ and $-20$ kPa representing water-filled capillary pore sizes less than 6 and 15 $\mu$m, respectively, than at $-3$ and $-10$ kPa. Microbivorous (fungivorous+bacterivorous) nematode abundance per unit mass of soil was not significantly different among matric potentials. Body diameters of nematodes ranged from 9 $\mu$m to 40 $\mu$m. We discuss several alternatives to the *exclusion hypothesis*, such as the '*enclosure hypothesis*' which states that nematodes may become trapped in large water-filled pore spaces even when capillary pore diameters (as computed from matric potential) are smaller than body diameters. One of the expected outcomes of grazing in enclosures is the acceleration of nutrient cycling.

## Introduction

Grazing of microorganisms by soil microfauna accelerates nutrient mineralization (Elliott et al., 1980; Ingham et al., 1985; Woods et al., 1982) contributing up to 30% to N mineralization (Hunt et al., 1987; Verhoef and Brussard, 1990). Microbivorous soil animals directly contribute to nutrient mineralization by egesting mineral nutrients derived from their forage (Darbyshire et al., 1994) and indirectly by affecting microbial growth rates (Bengtsson et al., 1993) and changing the structure of the microbial community (e.g., Griffiths 1994; Wardle and Yeates, 1993).

For microbivorous soil animals to influence nutrient mineralization directly or indirectly, the habitat of microorganisms and microbial grazers must overlap (Elliott et al., 1980; Hassink et al., 1993). Habitat for the most numerous groups of soil animals, protozoa and nematodes, comprises water-filled pore spaces, which expand and shrink with soil wetting and drying. Wallace (1958) observed three types of water-filled spaces: (1) the region surrounding a soil

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particle containing thin films of adsorbed water, (2) capillary water and (3) water held in meniscuses around the contact points of grains. This classification agrees with physical theory (Marshall and Holmes, 1992; Schachtschabel et al., 1992). Adsorbed water films are 1 to 5 nm thick (Marshall and Holmes, 1992; Schachtschabel et al., 1992). The dimensions of water meniscuses depend on grain size, shape and the nature of intergranular contact. The volume of water-filled capillaries depend on matric potential and pore structure. The availability of habitat for bacteria, nematodes and protozoa is thought to depend on pore size distribution and, thus, on texture (Hassink et al., 1993; Postma and van Veen, 1990). Pore size distributions are often measured as the soil moisture characteristic function which relates water-filled capillary volumes to matric potential from which pore size can be derived. The habitable pore space hypothesis states that soil animals can only access water-filled pores with diameters greater than their body diameter (Elliott et al., 1980; Hassink et al., 1993; Killham et al., 1993; Postma and van Veen, 1990; Wallace, 1958). As soil dries, water is held in increasingly smaller pores excluding nematodes and protozoa from an increasing proportion of the soil habitat. As a result, the contribution of grazers to mineralization is expected to decrease as soil dries. We term this interpretation of grazing in a porous environment the '*exclusion hypothesis*'.

The *exclusion hypothesis* may not always be an appropriate model of grazing in the soil environment. Soil nematodes and protozoa exist at low matric potential even when neck diameters of water-filled pores, as estimated by cylindrical capillary models, are smaller than the animal body diameter (Griffiths et al., 1995). In soils, pore structure is a three-dimensional network of pore chambers connected by constrictions (Glasbey et al., 1991). Griffiths et al. (1995) suggested that, in such a structure, nematodes may become trapped, or enclosed, in large water-filled chambers with diameters greater than nematode diameters. Enclosures remain saturated and become isolated from other water-filled spaces as soil dries (Figure 1). Enclosing microbivorous nematodes and microorganisms in isolated pore spaces may increase grazing pressure locally which may alter energy and nutrient fluxes within the soil food-web. We call this interpretation of how grazing affects biogeochemical cycles the '*enclosure hypothesis*'. Isolated water-filled spaces that make up enclosures may be similar to the soil microhabitat defined by Hattori (1994), the aggregatusphere/porosphere defined by Beare et al. (1995), or to pores that retain immobile water (Addiscott, 1977; Rao et al., 1980).

We investigated the effect of habitable pore space changes due to matric potential variation by measuring C and N mineralization, nematode abundance, and microbial biomass C at four different matric potentials ($-3$, $-10$, $-20$ and $-50$ kPa, corresponding to 100, 30, 15 and 6 $\mu$m capillary diameter). We used intact, undisturbed soil cores from an old field. Based on the exclusion hypothesis, we expected that nematode abundance, C and N mineralization rates would decrease with matric potential.

## Materials and methods

### *Study site and sample incubations*

We conducted a laboratory study using intact soil cores taken from an old field at the University of Rhode Island's Agricultural Experiment Station (Kingston, RI). The field is dominated by perennial grasses on a Hinckley sandy loam. Soil organic matter content was 5.3% (by loss-on-ignition), soil pH was 5.2 (Hendershot et al., 1993), bulk density was 1.05 g/cm$^3$ (from oven dry weight and core dimensions), and matric potential at field capacity was $-10$ kPa (Görres and Gold, 1996). A 20-m by 40-m plot was established and subdivided into fifty, 4-m by 4-m plots. Cores were taken from forty randomly selected plots in May 1997. The soil temperature (at 5 cm), air temperature and volumetric soil moisture were 14 °C, 18 °C, and 17%, respectively. Each sampling location was selected randomly within a plot. Three abutting, undisturbed soil cores (5-cm in diameter and 10-cm long) arranged in an equilateral triangle, were collected by pounding cores into the soil and extracting them by hand at each sampling site. Ten pairs of cores each were equilibrated to $-3$, $-10$, $-20$ and $-50$ kPa matric potential after saturation on sand and kaolin soil tension tables. When stable moisture contents were achieved after 7 days, i.e., when the 24-hour weight change was less than 1% of core weight, cores were incubated in 900-mL preserving jars at 14 °C in the dark. The first set of cores, comprising one of each pair, was removed from the jars after 21 days, after $CO_2$ evolution rates had become constant, and set aside to provide soil for an initial estimate of inorganic N. The second set was removed after 49 days incubation for a final estimate of inorganic N. Soil from

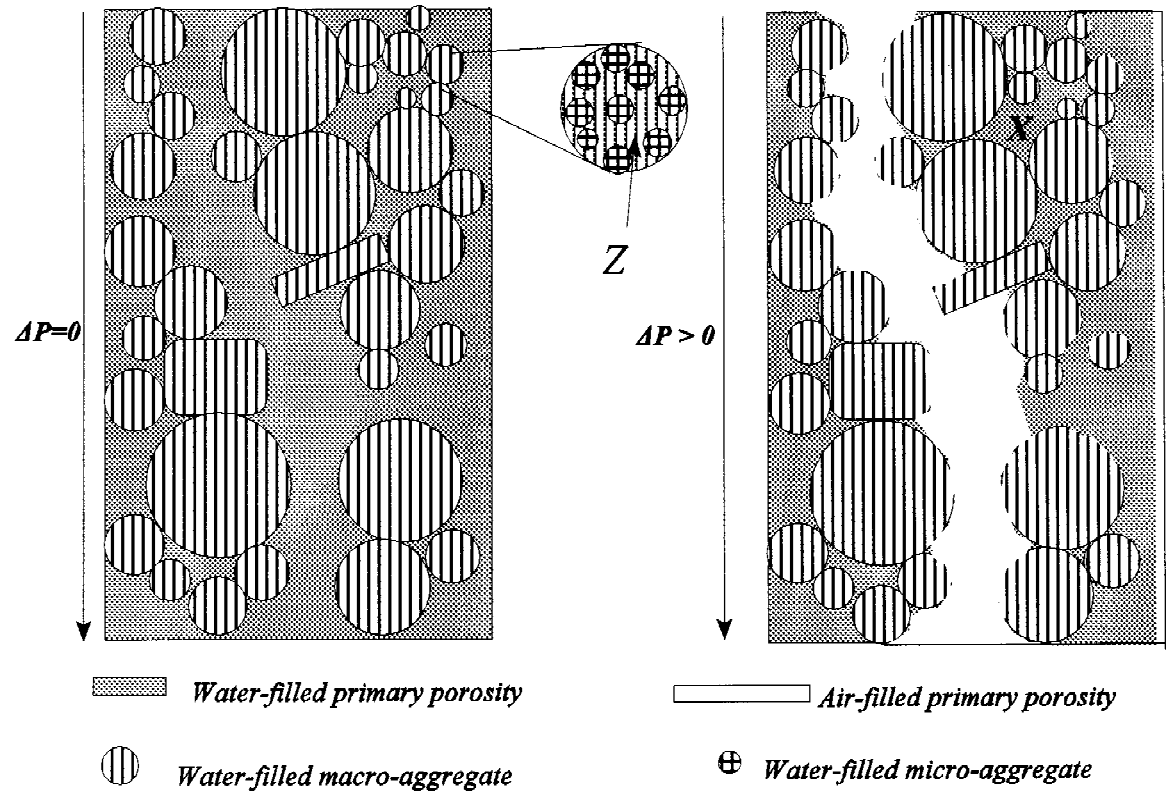


*Figure 1.* Formation of enclosures as a result of displacement of water (dark areas) from capillaries. (A) Saturated soil matrix at high matric potential. (B) Soil water distribution at low matric potential after capillary drainage of a large pore channel leaving water in aggregates (Z) and some inter-aggregate spaces (X).

each core was homogenized by shaking thoroughly by hand in a plastic sample bag (Neher and Cambell, 1994). We obtained gravimetric soil moisture from the difference between fresh weight and oven dry weight. We calculated volumetric soil moisture by multiplying gravimetric moisture and bulk density.

*C mineralization, biomass C and the metabolic quotient*

Carbon mineralization rates were derived from $CO_2$ concentrations measured weekly with gas chromatography (Görres et al., 1997) during the second incubation. Microbial biomass C was determined with the fumigation-extraction method (Vance et al., 1987) using 20 g (fresh weight) of soil for the first and the second set of cores. The C content of the extracts were determined using an automated Total Organic Carbon (TOC) analyzer (Shimadzu TOC 5000). To obtain microbial biomass C, the amount of C per g of dry soil in the unfumigated soil was subtracted from the value of the fumigated sample and the difference multiplied by a correction factor of 2.64 (Vance et al., 1987). We estimated microbial biomass C at the mid-point of the second incubation by calculating the average value from the values at the end of the first and the second incubation. The metabolic quotient, $q_{CO2}$ was calculated from C mineralization, $C_{min}$, measured for the second incubation period and the mid-point microbial biomass C, $C_{mic}$, using the expression

$$q_{CO_2} = \frac{C_{min}}{C_{mic}} \quad (1)$$

An increase in $q_{CO2}$ may reflect a diversion of energy from growth to maintenance of biomass when the microbial community is stressed (Anderson and Domsch, 1993).

*Inorganic C and N mineralization rates*

Inorganic N ($NH_4^+$-N and $NO_3^-$-N) concentrations were determined by extracting 1 g of soil with 10 mL of 2 *N* KCl solution (Keeney and Nelson, 1982),

filtering and colorimetric analysis of the filtrate using an automated nutrient analyzer (model RFA 300, Alpkem). Net N mineralization rates ($N_{min}$) were computed from initial and final incubations as

$$N_{\min} = \frac{(NO_3 - N + NH_4 - N)_{\text{final}} - (NO_3 - N + NH_4 - N)_{\text{init}}}{28} \quad (2)$$

*Nematode enumeration*

Nematodes were classified to family and enumerated to obtain the abundance of trophic groups. The extraction procedure and assignment of families to trophic groups are described by Neher et al., 1999 (this issue). Nematode diameter and lengths were measured from video projections of individual nematodes. Sample sizes were determined to allow for a 10% interval of the population mean with 95% confidence.

*Pore size determinations*

Pore size distributions for the soil cores extracted from the old field were derived from soil moisture characteristic curves measured from undisturbed cores with soil tension tables (Eijkelkamp, Giesbeek, The Netherlands). The effective pore diameter, D ($\mu$m), of a pore channel dewatered at pressure difference $\Delta$P (kPa) is given by the capillary rise equation (Hillel, 1971):

$$D = \frac{300}{\Delta P} \quad (3)$$

A series of volumetric moisture determinations at increasing pressure differences across initially saturated soil cores gives a pore size distribution by pore volume.

*Statistical analysis*

Student's *t* tests were used to determine whether nitrogen mineralization rates were significantly different from zero. Analysis of variance followed by multiple comparisons with *Bonferroni's t* test was used to determine if there were significant differences between means at different matric potentials when the data were normally distributed (SigmaStat for DOS, Jandel Scientific, San Rafael, CA.). When the data were not normally distributed, ANOVA (*Kruskal-Wallis* on ranks) followed by multiple comparisons with *Dunn's test* was used (SigmaStat for DOS, Jandel Scientific, San Rafael, CA.) to determine differences among matric potential treatments. Significance was evaluated at the 95% level.

## Results and discussion

*Nematode abundance*

The soil moisture characteristic curve (SMCC) for the matric potential interval from $-3$ to $-50$ kPa is shown in Figure 2A. Soil moisture values decreased monotonously from 0.30 at $-3$ kPa to 0.18 volumetric moisture at $-50$ kPa, corresponding to water-filled porosity of 50 to 30%, respectively. Volumetric moisture values differed significantly between all matric potentials except for between $-20$ and $-50$ kPa.

Microbivorous nematode abundance is shown in Figure 2B. Microbivore abundance was not significantly different between soils incubated for 21 and 49 days. We expected to see a decrease in microbivorous nematodes with decreasing matric potential. However, microbivore (fungivorous and bacterivorous nematodes) abundances did not differ significantly between matric potentials.

Figure 3 shows the cumulative distribution function of microbivorous nematode diameters, which varied between 9 and 36 $\mu$m. The exclusion hypothesis predicts that nematodes should be excluded from the soil when water-filled pore sizes become smaller than nematode diameters. In our experiment, $-3$, $-10$, $-20$ and $-50$ kPa correspond to water-filled pore sizes of $<100$, $<30$, $<15$ and $<6$ $\mu$m. Based on the cumulative distribution function of microbivorous nematode diameters, the exclusion hypothesis predicts that 100%, 95%, 10% and 0% nematodes would be excluded at $-50$ kPa, $-20$ kPa, $-10$ kPa and $-3$ kPa matric potential, respectively. We observed the same microbivore abundance at all matric potentials with no evidence of exclusion. There are three possible reasons why nematodes survived at low matric potentials ($-20$ and $-50$ kPa).

*(1) Survival due to biological adaptations*

Some nematode species have adaptations which allow them to survive dry periods in anhydrobiosis, which can be triggered at matric potentials as high as $-10$ kPa, although only a few individual microbivorous nematodes were observed to enter this state at matric potentials greater than $-300$ kPa in a study by Demeure et al., 1979. In their study, the onset

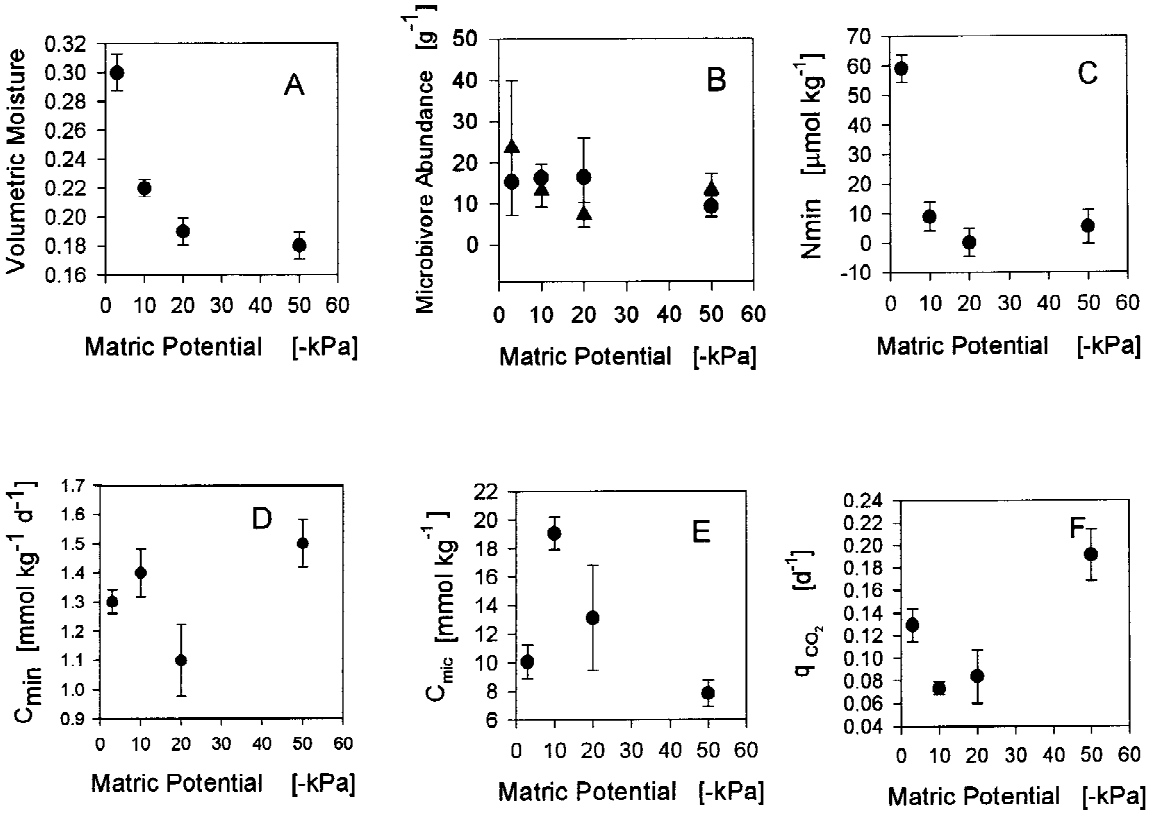


*Figure 2.* (A) Volumetric moisture, (B) microbivore abundance (● initial incubation, ▲ final incubation), (C) N mineralization ($N_{min}$), (D) C mineralization ($C_{min}$), (E), microbial biomass C ($C_{mic}$), and (F) $q_{CO_2}$ as functions of matric potential. Error bars represent 1 standard error.

of anhydrobiotic coiling in an *Aphelenchus* species (fungal-feeding) and in *Acrobeloides* spp. (bacterial-feeding) was dependent on moisture content rather than matric potential. A small fraction of nematodes formed coils at about 6% gravimetric moisture but the majority coiled at 4% gravimetric moisture. In our study, taxa that have this adaptation were present at all matric potentials (Neher et al., this issue). We did not assess whether these nematodes entered an anhydrobiotic state at any of our matric potential treatments. But, there are several differences between the soils used by Demeure et al. (1979) and those used in our study. Demeure et al. (1979) worked with soils with less water retention than our soils. The SMCC for Demeure et al. (1979) is consistent with soils with little aggregation and low organic matter. Gravimetric moistures at saturation were 37 and 28% for a sandy loam (sl) and a loamy sand (ls) respectively. At −10 kPa, gravimetric moistures were 16% (sl) and 6% (ls). At −50 kPa, moistures were 5.8% (sl) and 2.9% (ls). In our study, gravimetric moistures were 54%, 27%, 20%, 18% and 17% at 0, −3, −10, −20 and −50 kPa, respectively. The greater water retention in our soil suggests greater aggregation than for the soil used by Demeure et al. (1979). The effect of moisture on anhydrobiosis found by Demeure et al. (1979) suggest that at moisture values observed in our study, even at −50 kPa, anhydrobiosis is unlikely to have inactivated microbivorous nematodes.

*(2) Survival in enclosures*

Griffiths et al. (1995) found nematodes at matric potentials as low as −1000 kPa, at which nematodes should have been excluded. They hypothesized that nematodes may become trapped or enclosed in pores with large diameters that remain water-filled even at low matric potentials. Griffiths et al. (1995) explanation is consistent with soil physical theory, which predicts a division between mobile water, residing in inter-aggregate macro-pores, and immobile water, residing in soil aggregates (Addiscott et al., 1977; Rao et al., 1980). Immobile water within aggregates

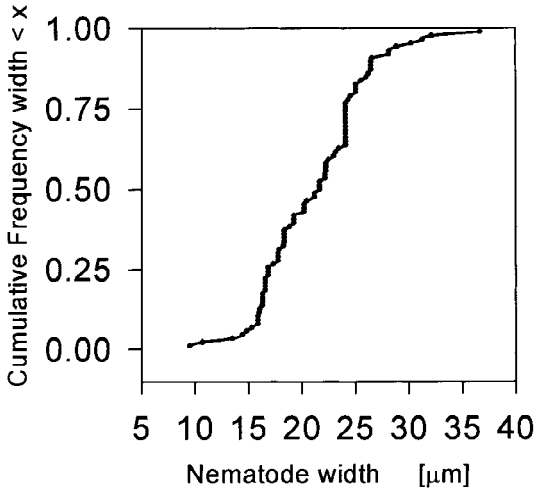


*Figure 3.* Cumulative frequency distribution of microbivorous nematode diameter.

may be a place where soil microfauna can reside even at low matric potentials. The possible biological importance of the threshold between intra-aggregate and inter-aggregate space has been emphasized by the '*microhabitat*' concept described by Hattori (1994) and the '*aggregatusphere*' concept by Beare et al. (1995). Glasbey et al. (1991) estimated that 17% of pores in an aggregate are large enough to be occupied by protozoa with a 20-$\mu$m dia., but only 11% of pores were accessible by protozoa through constrictions connecting the inside of the aggregate with inter-aggregate spaces. Nematodes may also fit into intra-aggregate pores. Sano and Nakasono (1997) found that J2 larvae of *Meloidogyne incognita* migrated from inter-aggregate spaces into aggregates at $-10$ kPa matric potential, showing that aggregates are microhabitats for nematodes.

Enclosures would be associated with particle aggregation. Aggregation may occur via two processes. A weak form of aggregation may occur when individual grains of silt, sand and clay are placed randomly and independently in space to build a three-dimensional structure. If this structure was sampled by extracting samples of equal volume from different locations in the structure, some samples contain more grains than others. This form of aggregation may occur in soils with little structure like the soil used by Demeure et al. (1979) and corresponds to the Boolean soil pore model (Horgan and Ball, 1994) and may be parameterized by a Poisson distribution as described for point processes in Cox and Isham (1980). In more structured soils, aggregation may be a result of processes that distribute grains relative to an ordering, or 'contagion', processes such as imposed on soil structure by earthworms (Lee, 1985), roots and polysaccharides (Tisdale and Oades, 1982). The statistics of contagious point processes are described in Cox and Isham (1980).

We hypothesize that enclosures form in soil with strong aggregation. In our study, enclosures may form as a result of water being expelled by a pressure difference applied across a core. Only water residing in pores that are connected along the pressure gradient, $\Delta$P (kPa), from the top of the core to the bottom will be evacuated if the narrowest constriction has a hydraulic diameter (cross-sectional area to wetted perimeter ratio), D ($\mu$m),

$$D > \frac{300}{\Delta P} \tag{4}$$

Figure 1 shows a diagram of an imaginary 'core' comprising micro and macro-aggregates and inter-aggregate pores. When a pressure difference is applied to the saturated core, large pores evacuate in accordance with the condition in Equation (4) and isolated pockets of water form. Some enclosures are associated with aggregates (location Z), others may be associated with inter-aggregate spaces (location X). If the entry pores into enclosures are large enough to allow colonization by nematodes under wet conditions, they may become trapped in the enclosures when soil dries.

When the soil wets up, enclosures may remain isolated to higher matric potentials than when they were formed because of soil moisture hysteresis. Pores with non-uniform diameters along their length are evacuated at matric potentials corresponding to narrow pore necks, but wet up at a higher matric potential, corresponding to large pore diameters, than when they were evacuated.

*(3) Survival in water-films associated with grains*

Another possible explanation of nematode survival at low matric potentials is that they remain active in meniscuses near the contacts between grains. Wallace (1958) observed movement of nematodes through a mono-layer of grains suspended in water from the surface of a Petri dish. Wallace (1958) observed that nematodes apparently migrate within capillaries that are only partially filled with water, held at the contacts between grains. However, by suspending a mono-layer of sand grains from the wetted surface of a Petri dish, the meniscuses of interstitial water may have been distorted and covered a greater area in the study by

Wallace (1958) than they would have in a soil. Nematode migration in the plane of the Petri dish surface observed by Wallace (1958) with partially filled capillaries may have been through capillary water held between the grains and the Petri dish which would represent a more connected network of water than created by the interstitial meniscuses at grain contacts that were apparent to Wallace (1958). If connected water-films are sufficiently thick to support nematode movement, they may also act to enhance grazing because Wallace (1958) found that nematodes moved more rapidly under conditions when in-plane capillaries were partially filled with water. This would result in more efficient foraging. In addition, meniscuses at grain contacts may trap nematodes close to pore surfaces on which, in real soil, bacteria may grow (Postma and van Veen, 1990), reducing the grazer-bacteria distance.

*C and N mineralization and grazing*

Grazing has been shown to have a considerable effect on mineralization (Elliott et al., 1980; Ingham et al., 1985; Woods et al., 1982). The survival of nematodes at $-50$ kPa suggests that the effect of grazing may not have been governed by the exclusion of nematodes from capillary pores. In accordance with the exclusion hypothesis, we expected that C and N mineralization rates would be faster at high (less negative) matric potentials than at low (more negative) matric potentials. C mineralization (Figure 2D) ranged from 1.1 mmol $kg^{-1}$ $d^{-1}$ (at $-20$ kPa) to 1.5 mmol $kg^{-1}$ $d^{-1}$ (at $-50$ kPa). These values are in agreement with C mineralization values measured for the same field two years earlier (Görres et al., 1998). The C mineralization rate at $-50$ kPa was greater than at $-20$ kPa, but not significantly different from values at $-3$ and $-10$ kPa (Figure 2D). Net N mineralization at $-3$ kPa was significantly greater at $-10$, $-20$ and $-50$ kPa (Figure 2C). Net N mineralization was positive only at $-3$ kPa which appears consistent with the *exclusion hypothesis.*

However, our N mineralization data can also be consistent with the enclosure hypothesis. Drury et al. (1991) hypothesized that N mineralization and immobilization are separated spatially. In enclosures, nutrient diffusion is limited to spaces within the enclosures. Any N mineralized by microbivorous nematodes becomes available locally for microbial growth in the enclosure. The consequence of enclosing grazers and microorganisms in aggregates is that the direct effect of grazing on N mineralization would be confounded by microbial immobilization of N, resulting in apparently low net mineralization rates.

We also expected, in agreement with the exclusion hypothesis, that microorganisms would be more protected from grazing at $-50$ kPa than at higher potentials ($-3$, $-10$ and $-20$ kPa), although Postma and van Veen (1990) regarded 3 $\mu$m (equivalent to $-100$ kPa) as the upper pore size limit of protection against predation by protozoa. Microbial biomass C was lower at $-50$ kPa than at $-10$ kPa, but not significantly different from biomass C at $-3$ and $-20$ kPa (Figure 2E). It is possible that microbial populations become substrate limited at low moisture contents which may account for less biomass at $-50$ kPa. However, at $-50$ kPa, C mineralization had not declined indicating that the biomass probably was not limited by substrate availability.

The metabolic quotient, $q_{CO2}$, which measures C mineralization per unit microbial biomass C, was significantly greater at $-50$ kPa than at the other matric potentials. Anderson and Domsch (1993) suggested that stressed microbial communities become less efficient C users, increasing $q_{CO2}$. The reduction of substrate diffusion at low moisture values (Griffin, 1981) may be such a stressor. However, we suggest that increased $q_{CO2}$ values may also be an outcome of grazing. When microbial growth is dependent on population density (e.g., in the logistic growth model) microbial biomass loss caused by grazing results in regrowth as long as sufficient substrate is available. The standing crop of biomass C may respond differently to grazing. If microbial biomass C decreased or remained constant under grazing, a greater $q_{CO2}$ value may result.

The significantly greater $q_{CO2}$ value at $-50$ kPa may be explained by increased grazing pressure on the microbial community that may occur when nematodes are trapped in enclosures. Specifically, by limiting the space in which nematodes can search for their food to aggregates that act as enclosures, foraging efficiency may increase. This argument appears to contradict the findings of Young et al. (1994) who investigated the effect of structure on predator-prey distances in liquid culture. They measured the distances between protozoan grazers and their bacterial food resource in a liquid culture and in a structured environment created by adding glass beads or sand to the liquid cultures. As particles were added to the culture the protozoan population diminished, with the protozoan population decreasing with particle size. This occurred because

the search time per unit volume increased, as structure is introduced, presumably because search paths become more tortuous. The investigation by Young et al. (1994) is different from, and not contradictory to, our study in that the structure introduced by adding beads or sand to liquid culture was maintained at saturation and that there was no contagious aggregation involved in forming structure. In our study, we used intact soil cores with aggregates and attempted to measure the effect of water-filled pore structure on nematode community composition and bio-geochemistry. By reducing habitable pore space, we reduced the search volume of grazer organisms. Aggregate enclosures, which have smaller pore sizes than the inter-aggregate macro-pores, and, thus, greater surface areas which bacteria can colonize (Hassink et al., 1993; Postma and van Veen, 1990), would focus grazing and foraging in a limited but possibly resource-rich search area, making grazing more efficient.

Grazing efficiency may also increase as a result of chemotaxis. Young et al. (1998) investigated whether nematodes would respond to the presence of a resource by preferentially migrating to the location of the resource. They found that *Caenorhabditis elegans* migrates through a porous, non-aggregated medium and gathers in places where food resources (*Escherichia coli*) are present, especially at high matric potential ($-0.5$ kPa). The effect of chemotaxis became less evident at lower matric potentials ($-4$ kPa). Similar results were found in the absence of soil particles by Andrews and Nicholas (1976). In the study by Young et al. (1998), grazers and *E. coli* cells were initially separated within a medium with mono-disperse, unaggregated particle size distributions. *E coli* was concentrated 4 cm away from the *C. elegans*. In the natural soils used by us, the separation of grazers and their resource is likely to be of much shorter scale. The importance of chemotaxis on grazing pressure under natural conditions may also be greatest at high matric potentials ($-0.5$ kPa) and may guide nematodes at very wet conditions. The effect of chemotaxis may diminish quickly, as observed by Young et al. (1998), as matric potential decreases.

Soil structure may have considerable impact on nutrient cycling in soil food-webs. However, few studies have given consideration to the effect of soil aggregation on trophic interactions under dynamic climate conditions. More experimentation elucidating the structure of below-ground habitat and its dynamic nature may improve our understanding of the effect of soil structure on trophic transfers of energy and nutrients.

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## References

Addiscott T M 1977 A simple computer model for leaching in structured soils J. Soil Sci. 28, 554–563.

Anderson T-H and Domsch K H 1993 The metabolic quotient for $CO_2$ ($q_{CO2}$) as a specific activity parameter to assess the effects of environmental conditions, such as pH, on the microbial biomass of forest soils. Soil Biol. Biochem. 25, 393–395.

Andrew A P and Nicholas W L 1976 Effect of bacteria on dispersal of *Caenorhabditis elegans* (Rhabditidae). Nematologia 22, 451–461.

Beare M H, Coleman D C, Crossley Jr. D A, Hendrix P F and Odum E P 1995 A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant Soil 170, 5–22.

Bengtsson G, Hedlund K and Rundgren S 1993 Patchiness and compensatory growth in a fungus-Collembolan system. Oecologia 93, 296–302.

Cox D R and Isham V 1980 Point Processes. Monographs on Applied Probability and Statistics. Chapman and Hall, London, UK.

Darbyshire J F, Davidson M S, Chapman S J and Ritchie S 1994 Excretion of nitrogen and phosphorus by the soil ciliate *Colpoda steinii* when fed the soil bacterium *Arthrobacter* sp. Soil Biol. Biochem. 26, 1193–1199.

Demeure Y, Freckman D W and van Gundy S D 1979 Anhydrobiotic coiling of nematodes in soil. J. Nematology 11, 189–195.

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

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

Glasbey C A, Horgan G W and Darbyshire J F 1991 Image analysis and three-dimensional modeling of pores in soil aggregates. J. Soil Sci. 42, 479–486.

Görres J H and Gold A J 1996 Incorporating spatial variability into GIS to estimate nitrate leaching at the aquifer scale. J. Environ. Qual. 25, 491–498.

Görres J H, Savin M C and 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.

Görres J H, Dichiaro M J, Lyons J B and 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.

Griffin D M 1981 Water potential as a selective factor in the microbial ecology of soils. *In* Water potential relations in soil microbiology. Ed. L F Elliott. pp 141–151. SSSA Spec. Publ. 9. SSSA, Madison, WI.

Griffiths B S 1994 Soil nutrient flow. *In* Soil protozoa. Ed. J F Darbyshire. pp 65–91 CAB International, Oxford, UK.

Griffiths B S, Young I M and Caul S 1995 Nematode and protozoan dynamics on decomposing barley leaves incubated at different matric potentials. Pedobiologia 39, 454–461.

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

Hattori T 1994 Soil microenvironment. *In* Soil Protozoa. Ed. J F Darbyshire. pp 43–64 CAB International, Oxford, UK.

Hendershot W H, Lalande H and Duquette M 1993 Soil reaction and exchangeable acidity. *In* Soil sampling and methods of anaiysis. Ed. M R Cater. Lewis Publishers, Boca Raton.

Hillel D 1971 Soil and water: Physical Principles and Processes. Academic Press, New York, NY, USA.

Horgan G W and Ball B C 1994 Simulating diffusion in a Boolean model of soil pores. Eur. J. Soil Sci. 45, 482–491.

Hunt H W, Coleman D C, Ingham E R, Ingham R E, Elliott E T, Moore J C, Rose S L, Reid C P P and Morley C R 1987 The detrital food web in a short-grass prairie. Biol. Fert. Soils 3, 57–68.

Ingham R E, Trofymow J A, Ingham E R and Coleman D C 1985 Interactions of bacteria, fungi, and their nematode grazers: Effect on nutrient cycling and plant growth. Ecol. Monogr. 55, 119–140.

Keeney D R and Nelson D W 1982 Nitrogen – Inorganic forms. I: Page A L, Miller R H and Keeney D R (Eds) Methods of soil analysis, Part 2. ASA, SSSA, Madison, WI.

Killham K, Amato M and Ladd J N 1993 Effect of substrate location in soil and soil pore-water regime on carbon turnover. Soil Biol. Biochem. 25, 57–62.

Lee K E 1985 Earthworms: Their ecology and relationship with soils and land use. Academic Press, Sydney, Australia.

Marshall T J and Holmes J W 1992 Soil Physics. Cambridge University Press, Cambridge, UK.

Neher D A and Campbell C L 1994 Nematode communities and microbial biomass in soils with annual and perennial crops. Appl. Soil Ecol. 1, 17–28.

Postma J and van Veen J A 1990. Habitable pore space and survival of *Rhizobium leguminosarum* biovar *trifolii* introduced into soil. Microbial Ecology 19, 149–161.

Rao P S C, Rolston D E, Jessup R E and Davidson J M 1980 Solute transport in aggregated porous media: Theoretical and experimental evaluation. Soil Sci. Soc. Am. J. 44, 1139–1146.

Sano Z-I, Nakasono K 1997 Influence of size of soil aggregates on the survival of *Meloidogyne incognita* juveniles. Soil Microorganisms 49, 9–16.

Schachtschabel P, Blume H-P, Brümmer G, Hartge K-H and Schwertmann U 1992 Lehrbuch der Bodenkunde. Ferdinand Enke Verlag, Stuttgart, Germany.

Tisdale J M and J M Oades 1982 Organic matter and water-stable aggregates in soils. J. Soil Sci. 33, 141–163.

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

Verhoef H A and Brussard L 1990 Decomposition and nitrogen mineralization in natural and agroecosystems: The contribution of soil animals. Biogeochem. 1 175–211.

Wallace H R 1958 Movement of Eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm, *Heterodera schachterii*, Schmidt. Ann. Appl. Biol. 46, 74–85.

Wardle D A and Yeates G W 1993 The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs. Oecologia 93, 303–306.

Woods L E, Cole C V, Elliott E T, Anderson R V and Coleman D C 1982 Nitrogen transformations in soil as affected by bacterial-microfaunal interactions. Soil Biol. Biochem. 14, 93–98.

Young I M, Griffiths B S, Robertson W M and McNicol J W 1998 Nematode (*Caenorhabditis elegans*) movement in sand as affected by particle size, moisture and the presence of bacteria (*Escherichia coli*). Eur. J. Soil Sci. 49, 231–241.

Young I M, Roberts A, Griffiths B S and Caul S 1994 Growth of a ciliate protozoan in model Ballotini systems of different particle sizes. Soil Biol. Biochem. 26, 1173–1178.