Enregistrement scientifique n° **1375**
Symposium n° **9**
Présentation: **oral**

Drilosphere effects on soil organic matter dynamics and microbial activity: From priming to regulation

Les effets de la drilosphère sur la dynamique de la matière organique du sol et l'activité microbienne: de “priming” à la régulation

BROWN George (1,2), **BAROIS Isabelle** (1), **LAVELLE Patrick** (1,2)

(1) Instituto de Ecología, A.C., A.P. 63, Xalapa, Ver. 91000, MEXICO
(2) LEST-ORSTOM/Université Paris VI, 32 Av. Henri Varagnat, Bondy, 93143, FRANCE

The moment the soil enters into contact with an earthworm, both surficially and internally, physicochemical and biological changes take place. The drilophere represents the whole soil volume under earthworm influence including the body surfaces and the gut, as well as external structures (casts and burrows) created by earthworm activities and the associated microflora and fauna affected. The extent of the drilosphere and its particular characteristics depends on the species and ecological category composition and temporal dynamics of activity of earthworm communities. The type of soil habitat and quality and quantity of ingested materials affect gut processes, digestive systems and cast and burrow characteristics, thus drilosphere properties as well. In the guts of epigeics, anecics and endogeics, microbial activity (principally bacteria and actinomycetes) is primed by intestinal mucus (water soluble-C) secretions, increasing decomposition of ingested stable soil OM forms. Meanwhile, populations of other organisms (e.g., fungi, protozoa, nematodes) decline with digestion, liberating nutrients due to low assimilation efficiencies. In casts, microbial activity may be high, and populations increase temporarily (up to several weeks), but then decrease as the soil dries out, particularly in compact casts of some species (e.g., *Millsonia anomala*), ultimately resulting in OM “protection”. Finally, at the scales of years to decades, it appears that earthworms regulate OM incorporation and turnover rates, and reductions of total soil C-stocks.

Key words: drilosphere, earthworms, soil properties, microorganisms, organic matter dynamics, microbial activity
Mots clés: drilosphère, vers de terre, proprietés du sol, microorganismes, dynamiques de la matière organique, activité microbienne

Enregistrement scientifique nº **1375**
Symposium nº **9**
Présentation: **oral**

Drilosphere effects on soil organic matter dynamics and microbial activity: From priming to regulation

Les effets de la drilosphère sur la dynamique de la matière organique du sol et l'activité microbienne: de "priming" à la régulation

BROWN George (1,2)**, BAROIS Isabelle** (1)**, LAVELLE Patrick** (1,2)

(1) Instituto de Ecología, A.C., A.P. 63, Xalapa, Ver. 91000, MEXICO
(2) LEST-ORSTOM/Université Paris VI, 32 Av. Henri Varagnat, Bondy, 93143, FRANCE

INTRODUCTION

The concept of an earthworm "sphere" of influence is relatively recent and, despite the fact that earthworms have been modifying soil characteristics worldwide for millenia, it was only recently that soil scientists described vermic horizons and Vermisols, where earthworm influence on soils reach dramatic proportions.[25] The term "drilosphere" was originally coined by Bouché[7] to describe the zone 2mm thick around earthworm burrow walls, but Lavelle[28] expanded its meaning to include all soil (including microbial and invertebrate populations) affected by earthworm activities, i.e., externally produced earthworm structures (middens, burrows, diapause chambers, surface and below-ground casts), the earthworm surface in contact with soil and the internal microenvironment of the earthworm gut (Figure 1).

The drilosphere is constantly changing in space and time; as earthworms explore new (still unaltered) soil or re-alter soil previously processed by communities at different times in the past, the soil's physical, chemical and biological properties and processes are modified. The temporal dynamics are dependent on an earthworm community's periods of activity and how long it has been in place, while the spatial dynamics are controlled by the community's horizontal and vertical distribution. However, interactions with other organisms, or with state soil properties, may cause drilosphere effects to persist for a longer time or influence a wider area than that delimited strictly by a community's temporal and spatial distribution. These interactions (specifically with microorganisms) and their consequent effect on soil organic matter (OM) dynamics are the subject of this paper.

EARTHWORM ECOLOGICAL CATEGORIES AND THE DRILOSPHERE

Three ecological categories of earthworms (epigeics, anecics and endogeics) have been described, each of which creates drilospheres with differing characteristics. The functional role of epigeics is primarily that of litter transformers[29], like other litter invertebrates, while anecics and endogeics are soil ecosystem engineers, i.e., their impact on soils is great and may influence properties and processes at the ecosystem level.[29] The components of the drilospheres of each ecological category are described below.

Epigeics

These species live in and consume, comminute and digest (partially) surface litter, rarely ingesting soil particles. Therefore, the effects of epigeic earthworms are not truly drilospheric since soils are affected indirectly, via changes in the litter. Many studies have demonstrated the effects of epigeics on litter decomposition rates using either litter bags of different mesh sizes to exclude or include earthworms[15] or other methods.[19,39] This litter processing in natural systems results in greater nutrient leaching into the soil and reduced immobilization by surface-dwelling fungi.[2,42] In addition, further processing of the egested faeces by other organisms (or earthworm species), helps release nutrients still tied up in the cast's undigested organic fractions.

The speed of digestion of ingested materials depends on their quality and the ability of the species to breakdown different components of the materials either with enzymes produced by gut epithelia or via microbially-mediated "mutualistic" digestion. The latter occurs when microorganisms in the gut are stimulated or 'primed' by mucus production (easily assimilable organic-C) in the foregut, releasing enzymes which digest the more complex ingested organic materials. This process occurs widely in endogeic species,[31] but has only just recently been addressed for other ecological categories. Since epigeics feed purely on litter and generally have a short gut transit time (e.g., 2.5 hr for *E. fetida*[18]), they probably depend on a rapid response of gut microbes to aid in digestion. This phenomenon can be confirmed by the high amount of water-soluble OM (38.5 and 60%, respectively) produced in the anterior gut *of Eisenia andrei* and *Perionyx excavatus* feeding on coffee pulp in Mexico (Barois et al. unp. data). The temperatures at which digestion occurs is probably also important, with greater mucus production at higher temperatures (seen in endogeics[3]).

Epigeic earthworm guts preferentially stimulate some microorganisms, and reduce others. Phenomena occurring in other ecological categories, such as digestion of protozoa[10] and fungal hyphae,[14] release of antibiotics[24] and selective ingestion of microflora,[13] likely also occur in epigeic earthworm guts, leading to a relative dominance of microorganisms different to that found in uningested soils. For example, various *Vibrio* spp. and *Streptomyces lipmanii* were the dominant bacteria and actinomycetes in *Eisenia lucens* guts[12,34] but found in low abundance in its habitat (decomposing wood). Further research with other earthworm species, particularly in-vitro descriptions of gut microflora and processes, will help pinpoint the mechanisms by which epigeics differentially stimulate gut microflora species and their activity, and the resulting effects on cast properties and microfloral communities.

Anecics

These primarily vertically burrowing species are the dominant earthworms (in biomass) in many temperate region soils,[27] and often produce characteristic surface features called “middens.” This term, coined by Nielsen and Hole,[37] refers to the mixture of surface organic materials (principally leaves) and soil into a somewhat circular “mound-shaped” region around a surface burrow’s openning. Up to 90% of apple orchard and temperate deciduous forest leaf falls may be buried into the soil or transferred into *Lumbricus terrestris* middens,[22,40] and ca. 10% of this litter may be assimilated,[41] while 30% of annually decomposed grass litter may be incorporated into Lamto savanna soils by the tropical earthworm *Millsonia lamtoiana*.[26] Because of this, litter does not accumulate on the soil surface, and decomposition processes are accelerated forming humus of the mull type.

Middens appear to act as “external rumens,” where microbes and fauna attracted to this ‘hot-spot’ enhance decomposition of uningested litter and organic fragments in casts, which are then often reingested,[8] probably due to fungal colonization of these substrates[38] and then preferential feeding on these fungi.[13] In the gut of anecic earthworms, both direct (a few basic enzymes) and indirect (mutualistic) digestion processes are probably present. However, since few studies have described the enzymatic capacities and intestinal mucus production of anecics[31], other species must be tested to confirm this. Food digestion and low assimilation efficiencies, added to population turnover means that significant amounts of nutrients can circulate through and out of anecic tissues. Most accumulate in casts, while others are released in mucus or urine and in dead earthworm biomass. Estimates of the total amount of N recycled range from a few kg up to 100 kg ha^{-1}.[35]

Transit through *L. terrestris* guts has shown a differential stimulation or reduction in microbial populations: fungi and active protozoa (not cysts) are generally reduced but then rapidly multiply in casts, while bacteria and actinomycete populations tend to increase in both guts and casts, though this appears to be primarily due to increases in activity and culturability, and not population growth *per se*.[10] The priming of these organisms may release significant amounts of plant-available P and N in anecic drilosphere structures.

Contrary to epigeics that ingest only litter, anecics ingest significant proportions of soil ranging from 61% (*Lumbricus herculeus*[9]) up to 90% (*M. lamtoiana*[21]) depending on seasonal activity and litter quality and availability throughout the year. Litters of higher N content or colonized by particular fungi species are preferentially ingested.[1,13] When surface conditions are less favorable (e.g., little available food) or when constructing their burrows, anecics ingest more soil. Surface casting may thus reach 5 Mg ha^{-1} yr^{-1} [32] and the burrow system attain lengths of >100 m m^{-2} in a French pasture.[23]

The feeding and casting habits of anecics may deeply influence soil characteristics up to >1m depth. The translocation of litter, mucus excretions, air penetration and selection of soil particles enrich the burrow walls with oxidized Fe,[20] OM and plant-available nutrients (N, P, K, Ca[17]). Hence, even though this region covers a small part of the total soil volume,[23] burrow walls have higher microbial activities[43] and populations of ammonifying, denitrifying, free-living aerobic and anaerobic N-fixing, hemicellulolytic and pectinolytic bacteria[6] than surrounding un-processed soil. For these reasons, roots are often found preferentially using and proliferating in anecic earthworm burrows[16].

Dispersal of beneficial bacteria such as VAM, *Rhizobia* or other microorganisms, and elimination of plant pathogenic fungi may result in futher benefits to pertinent plants.[10]

Endogeics

These ecosystem engineers are the most prevalent earthworms (in biomass) in most tropical environments,[27] often being the only group present, particularly in agroecosystems. Endogeics are geophagous earthworms that feed on soil OM of different qualities (poly = high, meso = medium, oligo = poor), producing surface and below-ground casts of two main types: globular (compact, large) and granular (loose, small). Over 1000 Mg ha^{-1} yr^{-1} casts may be produced at Lamto savannas (mostly of *Millsonia anomala*), of which only about 2-3% are deposited on the soil surface.[26] Endogeic casts, with generally more clay and frequently more OM than uningested soil, contain and release significant amounts of nutrients; e.g., fresh casts of *Pontoscolex corethrurus* may have 2-8 times more inorganic P[33] and NH_4[5] than uningested soil. This N may result from selective ingestion of richer soil portions, microbial mineralization, enteronephridial N excretions or asymbiotic N_2 fixation in the gut.[4]

Endogeic digestion appears to be primarily mutualistic, with highly variable amounts of intestinal mucus being produced in the foreguts, depending on feeding groups and species.[31] Highest production was observed in poly- and meso-humic endogeics. Gut microflora are also preferentially stimulated or reduced depending on earthworm and microbe species, soil environment, and food ingested.[10] Fungal hyphae, active protozoa, algae, myxomycetes and nematodes may be digested, while encysted or protected forms survive gut passage and then rapidly proliferate in casts.[10] Cell viability is often positively affected so that higher populations of many microorganisms are detected in casts than bulk soils when using plate counts (CFU's) or other methods.[10] Microbial dispersal, such as VAM, *Frankia, Rhizobia* and other beneficial bacteria (e.g., biocontrol species, rhizobacteria), or plant pathogenic fungi and parasitic nematodes by endogeics is important but often overlooked in soil ecology and plant pathology[10].

Due to the diversity of interactions (enhancement, statis, reduction) between earthworms and microorganisms at various levels of the drilosphere, endogeics may have completely different effects on OM dynamics depending on the spatio-temporal viewpoint.[29]

(i) At the short term (a few hours) and small scale (casts and guts), earthworms selectively ingest and comminute particularly larger fractions, but only assimilate low proportions of OM (2-18%), thus egesting large amounts of C in casts and enhancing microbial activity (priming) in both the gut (with mucus-C) and casts.[30]

(ii) At the intermediate scales (several days to weeks; casts and burrows) microbial activity and populations in casts and burrows increase and then decrease[10] when available substrates are exhausted or the casts and burrows dry out, producing unfavorable environmental conditions. OM decomposition, particularly in casts, generally increases, releasing nutrients and CO_2 (and other gases), but may then decrease due to physical protection in compact casts (e.g., of *M. anomala*), reducing C mineralization up to 30%.[36]

(iii) At scales of years to decades in the soil profile, the role of endogeics is determined by the effects at the former scales. It appears that they stimulate an overall acceleration of OM turnover, yet cause slight decreases in total stocks. In a 7-year experiment with continuous maize in Yurimaguas, Peru, *P. corethrurus* inoculation resulted in a loss of 3.2 t ha^{-1} C higher than in uninoculated plots.[11]

CONCLUSIONS: PRIMING TO REGULATION

From the previous discussion we know that earthworms play a significant role in altering microbial communities and priming activity in the drilosphere. The extent of this effect and its interaction with soil OM dynamics depends on the type and spatial distribution of drilospheres produced by different ecological categories: epigeics are litter transformers and thus affect mostly surface-litter microbes and decomposition rates; anecics mix surface litter with soil accelerating surface OM incorporation and humification, and creating 'hot-spots' of microbial activity in middens and burrow walls; endogeics ingest large amounts of soil concentrating OM in the casts, dispersing microorganisms, and regulating microbial activity and OM dynamics (decomposition, turnover, total stocks) in both guts and casts through a balance of positive and negative reactions on these processes at different spatio-temporal scales. The consequences of this regulation on soil aggregation, plant nutrient availability, root 'health' and sustainability of crop yields are important and deserve further investigation.

REFERENCES

1- Abbott I & Parker C A. 1981. Interactions between earthworms and their soil environment. *Soil Biol. and Biochem.* 13, 191-197.
2- Anderson J M, Ineson P & Huish S A. 1983. The effects of animal feeding activities on element release from deciduous forest litter and soil organic matter. *In* Lebrun P, André H M, de Medts A, Grégoire-Wibo C & Wauthy G (ed.) *New trends in soil biology*. Dieu-Brichart, Louvain-la-Neuve. pp. 87-100.
3- Barois I. 1992. Mucus production and microbial activity in the gut of two species of *Amynthas* (Megascolecidae) from cold and warm tropical climates. *Soil Biol. Biochem.* 24, 1507-1510.
4- Barois I, Verdier B, Kaiser P, Mariotti A, Rangel P & Lavelle P. 1987. Influence of the tropical earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on the fixation and mineralization of nitrogen. *In* Bonvicini Pagliai A M & Omodeo P (ed.) *On Earthworms*. Mucchi, Modena. pp. 151-158.
5-Barois I, Lavelle P, Brossard M, Tondoh J, Martinez M A, Rossi J P, Senapati B K, Angeles A, Fragoso C, Jimenez J J, Lattaud C, Ka Kajondo J K, Blanchart E, Brown G & Moreno A G. 1998. Ecology of species with large environmental tolerance and/or extended distributions. *In* Lavelle P, Brussaard L & Hendrix P F (ed.) *Management of earthworm populations in tropical agroecosystems*. CAB International, Wallingford. in press.
6- Bhatnagar T. 1975. Lombriciens et humification: Un aspect noveau de l'incorporation microbienne d'azote induite par les vers de terre. *In* Kilbertius G, Reisinger O, Mourey A & da Fonseca J A C (ed.) *Humification et biodegradation*. Pierron, Sarreguemines. pp. 169-182.
7- Bouché, M B. 1975. Action de la faune sur les etats de la matiere organique dans les ecosystemes. *In* Kilbertius G, Reisinger O, Mourey A & da Fonseca J A C (ed.) *Humification et biodegradation*. Pierron, Sarreguemines. pp. 157-168.

8- Bouché, M B. 1983. Ecophysiologie des lombriciens: Aquis recents et perspectives. *In* Lebrun P, André H M, de Medts A, Grégoire-Wibo C & Wauthy G (ed.) *New trends in soil biology*. Dieu-Brichart, Louvain-la-Neuve. pp. 321-333.
9- Bouché M B & Kretzschmar A. 1974. Fonctions des lombriciens II. Recherches méthodologiques pour l'analyse qualitative de la matière organique végétale ingéré (etude du peuplement de la station R.C.P.-165/P.B.I). *Rev. Ecol. Biol. Sol* 11, 127-139.
10- Brown G G. 1995. How do earthworms affect microfloral and faunal community diversity? *Plant & Soil* 170, 209-231.
11- Charpentier F. 1996. Effet de l'inoculation du ver de terre *Pontoscolex corethrurus* sur la dynamique de la matière organique dans une culture continue de maïs en Amazonie péruvienne. PhD Thesis, Université Paris VI.
12- Contreras E. 1980. Studies on the intestinal actinomycete flora of *Eisenia lucens* (Annelida, Oligochaeta). *Pedobiologia* 20, 411-416.
13- Cooke A & Luxton M. 1980. Effects of microbes on food selection by *Lumbricus terrestris* L. *Rev. Ecol. Biol. Sol* 17, 365-370.
14- Dash H K, Beura B N and Dash M C. 1986. Gut load, transit time, gut microflora and turnover of soil, plant and fungal material by some tropical earthworms. *Pedobiologia* 29, 13-20.
15-Edwards C A & Heath G W. 1963. The role of soil animals in breakdown of leaf material. *In* Doeksen J & van der Drift J (ed.) *Soil organisms.* North Holland, Amsterdam. pp. 76-84.
16- Ehlers W. 1975. Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Sci*. 119, 242-249.
17- Graff O. 1967. Uber die verlagerung von nahrelementen in den unterboden durch regenwurmtatigkeit. *Landwirsch. Forsch.* 20, 117-127.
18- Hartenstein F, Hartenstein E & Hartenstein R. 1981. Gut load and transit time in the earthworm *Eisenia foetida*. *Pedobiologia* 22, 5-20.
19- Huhta V, Haimi J & Setala H. 1991. Role of fauna in soil processes: techniques using simulated forest floor. *Agric. Ecosystems Environ.* 34, 223-229.
20- Jeanson C. 1971. Structure d’une galerie de lombric a la microsonde electronique. *In* d’Aguilar J (ed.) *Organismes du sol et production primaire*. INRA, Paris. pp. 513-525.
21- Ka Kayondo J K. 1984. Ecologie alimentaire du ver de terre *detrivore Millsonia lamtoiana* (Acanthodrilidae-Oligochaeta) dans la savane de Lamto (Côte d'Ivoire). PhD Thesis, Universite Paris VI.
22- Knollenberg W G, Merritt R W & Lawson D L. 1985. Consumption of leaf litter by *Lumbricus terrestris* (Oligochaeta) on a Michigan woodland floodplain. *Am. Middl. Nat.* 113, 1-6.
23- Kretzschmar A. 1982. Description des galeries de vers de terre et variations sasonnieres des reseaux (observations en conditions naturelles). *Rev. Ecol. Biol. Sol* 19, 579-591.
24- Kristufek V, Ravasz K & Pizl V. 1993. Actinomycete communities in earthworm guts and surrounding soil. *Pedobiologia* 37, 379-384.
25- Langmaid K K. 1964. Some effects of earthwom invasion in virgin Podzols. *Can. J. Soil Sci.* 44: 34-37.
26- Lavelle P. 1978. Les vers de terre de la savane de Lamto (Côte d'Ivoire): Peuplements, populations et fonctions dans l'écosystème. Publications Laboratoire Zoologie ENS, Université Paris VI, no. 12.

27- Lavelle P. 1983. The structure of earthworm communities. *In* Satchell J E (ed.) *Earthworm ecology*. Chapman & Hall, London. pp. 449-466.
28- Lavelle P. 1987. The importance of biological processes in productivity of soils in the humid tropics. *In* Dickinson R E & Lovelock J (ed.) *Geophysiology of Amazonia*. Wiley & Sons, New York. pp. 175-214.
29- Lavelle P. 1997. Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. *Adv. Ecol. Res.* 24, 93-132.
30- Lavelle P & Gilot C. 1994. Priming effects of macroorganisms on microflora: A key process of soil function? *In* Ritz K, Dighton J & Giller K (ed.) *Beyond the biomass*. Wiley-Sayce, London. pp. 173-180.
31- Lavelle P, Lattaud C, Trigo D & Barois I. 1995. Mutualism and biodiversity in soils. Plant & Soil 170, 23-33.
32- Lee K E. 1985. Earthworms: Their ecology and relationships with soils and land use Academic Press, Sydney.
33- Lopez-Hernandez D, Fardeau J C & Lavelle P. 1993. Phosphorus transformations in two P-sorption contratsing tropical soils during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.* 25, 789-792.
34- Mariaglieti K. 1979. On the community structure of the gut microbiota *of Eisenia lucens* (Annelida, Oligochaeta). *Pedobiologia* 19, 243-252.
35- Marinissen J C Y & de Ruiter P C. 1993. Contribution of earthworms to carbon and nitrogen cycling in agro-ecosystems. *Agric. Ecosystems Environ.* 47, 59-74.
36- Martin A. 1991. Short-term and long-term effect of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidæ, Oligochaeta) of tropical savannas, on soil organic matter. *Biol. Fert. Soils* 11, 234-238.
37- Nielsen G W & Hole F E. 1964. Earthworms and the development of coprogenous A_1 horizons in forest soils of Wisconsin. *Soil Sci. Soc. Am. Proc.* 28, 426-430.
38- Parle J N. 1963. A microbiological study of earthworm casts. *J. Gen. Microbiol.* 31, 13-22.
39- Parmelee R W, Beare M H, Cheng W, Hendrix P F, Rider S J, Crossley D A & Coleman D C. 1990. Earthworms and enchytraeids in conventional and no-tillage agroecosystems: a biocide approach to assess their role in organic matter breakdown. *Biol. Fert. Soils* 10, 1-10.
40- Raw F. 1962. Studies of earthworm populations in orchards I: Leaf burial in apple orchards. *Ann. Appl. Biol*. 50, 389-404.
41- Satchell J E. 1967. Lumbricidae. *In* Burgess A & Raw F. (ed.) *Soil biology*. Academic Press, London. pp. 259-322.
42- Spiers G A, Gagnon D, Nason G E, Packee E C & Louiser J D. 1986. Effects and importance of indegenous earthworms on decomposition and nutrient cycling in coastal forest ecosystems. *Can. J. For. Res.* 16: 983-989.
43- Stehouwer R C, Dick W A & Traina S J. 1993. Characteristics of earthworm burrow lining affecting atrazine sorption. *J. Environ. Qual*. 22, 181-185.

Key words: drilosphere, earthworms, soil properties, microorganisms, organic matter dynamics, microbial activity
Mots clés: drilosphère, vers de terre, proprietés du sol, microorganismes, dynamiques de la matière organique, activité microbienne

Figure 1. Components of the drilosphere (in boxes) and some associated properties and processes.