

XI International Colloquium on Soil Zoology, Jyväskylä, Finland, 10-14 August, 1992

Soil changes during gut transit through *Octolasion lacteum* Oerley (Lumbricidae, Oligochaeta)

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Physico-chemical and biological measurements were carried out on gut contents and casts of *Octolasion lacteum*, an earthworm species frequently found in temperate regions of Northern Spain. The content of water, water-soluble organic matter and pH were increased in the anterior part of the gut. The water-soluble compounds decreased in the medium and posterior parts of the gut and were almost absent in casts. The mean oxygen consumption in the gut content increased about two to three times suggesting a microbial activation in the gut. These results support the hypothesis of a mutualistic digestion system also in temperate endogeic earthworms.

1. Introduction

Earthworm activities cause important modifications in physico-chemical and biological properties of soils, in particular in the drilosphere, affecting carbon cycling, microbial activity, nutrient release, soil aggregation and dynamics of organic matter. (Bhatnagar 1975, Lee 1985, Martin 1991 and Martin et al. 1992).

Measurements of several physico-chemical and biological parameters in the gut content of two endogeic mesohumic tropical earthworm species, *Millsonia anomala* and *Pontoscolex corethrurus* (Barois & Lavelle 1986, Barois 1987), indicate the existence of a mutualistic relationship between microflora and earthworms for the exploitation of soil organic matter. Similar observations carried out on the tropical oligohumic earthworm, *Dichogaster terrae-nigrae*, which feeds on deeper soil horizons, and two epigeic tropical species *Amyntas corticis* and *Amyntas gracilis*, (Barois & Lavelle 1986) suggest that mutualistic digestion generally occurs in tropical earthworms of different ecological categories (Martin 1988, Barois 1992). We (Trigo & Lavelle 1993), studied the same processes in a semiaquatic temperate earthworm, *Allolobophora molleri* concluding that a mutualistic digestion system is also present in this species. We also hypothesized that digestion is largely performed by the microflora of the ingested soil; the addition of high

amounts of water and water-soluble organic matter in the anterior part of the gut results in a dramatic increase in microbial activity, and further digestion of organic matter by these activated microorganisms. This process is analogous to the "priming effect" (Jenkinson 1966).

In this study we seek evidence of a similar mutualistic digestion system in an endogeic earthworm species living in temperate regions, by measuring some physico-chemical and biological parameters (water content, pH, microbial respiration and water-soluble organic matter) in noningested soil, in different parts of the gut and in fresh casts.

2. Material and methods

Specimens of *O. lacteum* and soil from the 0-15 cm layer were collected from an irrigated meadow at Rubio-Boqueixón (La Coruña, Spain) UTM 29TNG58. The soil had a content of sand, silt and clay of 38, 40 and 22%, respectively. The pH was 5.8, and the soil organic matter content was 9%. After sampling, the earthworms were kept in plastic boxes, fed with soil in which they had been collected, and sieved with a 2 mm screen; the culture temperature was maintained between 17 and 21°C.

Samples of gut content were obtained after killing the earthworms by immersion in boiling water for one second.

ORSTOM Fonds Documentaire

- 6 JUN 1995

N° : 41-696 2p1

Cote : B

The gut was cut behind the gizzard and divided into three parts: anterior (A); middle (M) and posterior (P). The gut content of each section was carefully removed to prevent any contamination with coelomic fluid and blood. The water-soluble organic matter content was measured combining the gut contents of the respective parts of the gut of three or four specimens; pH was measured with a special electrode which allows measurements "in situ" in the gut content. Water-soluble organic matter was extracted after dilution in water at 60°C, filtered through a 0.2 µm filter, freeze-dried and weighed. Some samples of gut content were dried over silica gel for 24 hours and used for water content determinations. Oxygen consumption in samples of gut material was measured with a microrespirometer (Verdier 1983) during 3 hours at 21°C. Sample size ranged between 10 and 50 mg. Measurements of redox potential in gut contents of *Pontoscolex coarctatus* have shown microaerophilic conditions, with decreasing values from the anterior to posterior part (Barois & Lavelle 1986). These results suggest that microbial respiration results in oxygen consumption in earthworm gut content, and so respirometric methods may be used to assess microbial activity.

The values of each factor in soil, casts and gut contents were compared using ANOVA test at 95 and 99% levels of significance.

3. Results

Water-soluble organic matter was below detection level in the soil and casts, but was produced in great amounts in the anterior part of the gut, reaching percentages of 28.5%. It decreased strongly in the middle and posterior part of the gut (3.1 and 1.8%, respectively, Fig. 1)

The pH of soil was 5.8; it increased significantly in the gut towards neutral values (7.0, 6.7, 6.5). A decrease to about 6.0 occurred in the casts, a slightly higher value than in control soil (Fig. 1).

The water content was higher in the gut and casts than in soil (54.9% in casts, 45.1% in soil) (Fig. 1).

Oxygen consumption was low in soil and casts, and increased strongly in the gut, with an increase from the anterior to the middle part, and a decrease in the posterior (Fig. 1).

Table 1 shows the results obtained using an ANOVA test.

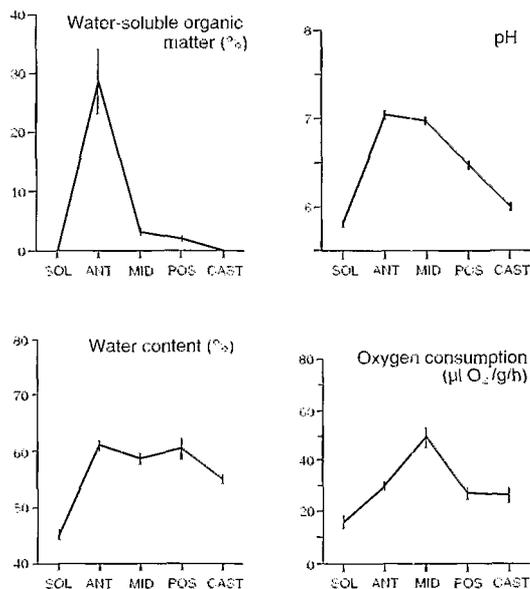


Fig. 1. Physico-chemical parameters measured in soil (SOL), casts (CAST) and gut contents (ANT, MID, POS) of *Octolasion lacteum*.

4. Discussion

The soil ingested by *O. lacteum* was considerably modified during the gut transit. The addition of large amounts of water and the intensive mixing in the gizzard resulted in homogenization of the soil, and presumably increased the contact between the microflora and organic substrate. As a result the metabolic activity was enhanced.

The amount of water-soluble organic matter was very high in the anterior gut, presumably due to the secretion of mucus by secretory gland cells in the pharynx and oesophagus (Philis Dales 1967, Michel & Devillez 1978). The concentration decreased quickly as mucus was transformed or consumed during digestion, presumably as a consequence of the intense metabolic activity of microorganisms (Lavelle et al. 1983, Martin et al. 1987). This process may be promoted by the addition of large amounts of water, which induces the dispersion of the soil matrix, which further enhances the

Table 1. Analysis of variance of water-soluble organic matter, pH, water content, and oxygen consumption in soil (S), anterior gut (A), midgut (M), posterior gut (P), and casts (C). * $P < 0.05$, ** $P < 0.01$; ns not significant.

	Water-soluble OM				pH				Water content				O ₂ consumption			
	A	M	P	C	A	M	P	C	A	M	P	C	A	M	P	C
S	**	ns	ns	ns	**	**	**	ns	**	**	**	**	**	**	*	*
A		**	**	**		ns	**	**		ns	ns	**		**	ns	ns
M			ns	ns			**	**			ns	*		**	**	**
P				ns				**				**				ns

accessibility of organic matter to soil microorganisms (Barois & Lavelle 1986). The intestinal mucus may not only function as an easily assimilable source of energy for microorganisms, it may also be a source of lytic enzymes, e.g. chitinases, cellulases and amylases (Loquet & Vincelas 1987, Laverack 1963) as proposed by Martin et al. (1987). After being hydrolyzed, part of this mucus may be reabsorbed by the worms simultaneously with the compounds produced by the degradation of soil organic matter. A rapid assessment of the amounts of energy required to produce the large quantities of mucus shows that part of it is necessarily reabsorbed and recycled within the earthworm.

The increase in soil pH during gut transit may be related to mucus production and to the activity of the Morren glands that secrete carbonates (Prentø 1979).

Results of the present study indicate that the digestion processes in the gut of *O. lacteum* are similar to those described for the tropical species *M. anomala* and *P. corethrurus* (Barois 1987, Barois & Lavelle 1986), *D. terrae-nigrae* (Martin 1988) and *Amyntas corticis* and *A. gracilis* (Barois 1992). Furthermore, this process is the same as that described for *A. molleri* (Trigo & Lavelle 1993), a semiaquatic oligochaete living in temperate climates. The soil ingested by the worm is enriched with large amounts of mucus and water in the anterior gut, while pH is neutralized. These processes result in an activation of microflora, which further digest soil organic matter in the middle and posterior parts of the gut. The earthworm may absorb assimilable organic matter released by digestion of the activated soil microflora. This hypothesis is supported by the fact that the amount of assimilable carbon is at a maximum in the anterior part of the gut, whereas the peak of microbial respiration was found in the medium and posterior parts.

The secretion of water-soluble organic components was considerably higher in the temperate species studied than in tropical ones. This may be due to lower soil temperatures in temperate zones, limiting the microbial activity, and thus a higher production of mucus is necessary to activate it, whereas in the tropical species, the higher temperatures allow a lower mucus production.

Regarding to the water content of the gut, the temperate worm *A. molleri* (Trigo & Lavelle 1993) shows a progressive increase along the gut, whereas *O. lacteum* tends to maintain it, with a slight decrease in casts. On the other hand, tropical species show a reduction of water content along the gut. Casts of *P. corethrurus*, a tropical earthworm from humid pastures, still retain 85% of the water contained in the anterior gut, and only 15% is reabsorbed. For *M. anomala*, a species living in humid savannas and subject to seasonal water stress, the water content of casts is only 50% of that measured in the anterior part of the gut. It seems clear that the changes during the gut transit are related to environmental conditions. In species under dry conditions, water retention processes are dominant, whereas in moist to wet environments water elimination processes predominate.

As a conclusion, the obtained results for *O. lacteum* agree with the existence of a mutualistic digestion system, as proposed by Barois & Lavelle (1986).

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