

M. B. BOUCHÉ, G. FERRIÈRE, P. SOTO

The role of earthworms in the decomposition and nitrogen nutrition of plants in a grassland

ABSTRACT

For the first time, the nitrogen flow through a soil animal has been measured in a grassland over a period of 40 days. The animal was *Nicodrilus longus longus* (Ude, 1886) in the adult stage. The paper deals with the extrapolation of these results to a full year thanks to the activity index directly calculated from field data. Extrapolation is also made to other stages and/or species of the same earthworm community. Earthworms play an important role in grassland plant nutrition (in spring they supply about 80% of plant needs).

The role of earthworms in the nitrogen cycle and in decomposition processes indicates that the classical nitrogen pattern commonly accepted in soil biology should be revised.

Key-words: Earthworm, grassland plant nutrition, nitrogen cycle.

1. Introduction

The International Biological Programme, started in 1963, aimed to understand better the functioning of ecosystems and within this programme the earthworms were studied as to their role in the economy of nature. The first approximations (Satchell, 1963) showed that earthworms play a considerable role on the transfer of elements and that prompted us to attempt to quantify this role. Unfortunately, this could only be estimated indirectly and the proof that it was important remained all the more doubtful as only few agronomists, pedologists or ecologists have been (or are) aware of it.

Today the situation has not improved because of the lack of funds devoted to these studies; however, there is a considerable difference: today techniques are available to study this role, and the first results obtained, as incomplete as they may be, already evidence two facts:

- the role of the earthworms is much more important and decisive than was previously thought and has obvious economical implications.

– Pedozoology, long a late imitator of the «energy balances» and of the «cycles of elements» described by the plant ecophysiologicalists (Eckhart, 1972) and by microbiologists is today a driving discipline for the understanding of the real (= *in situ*) root and microbial life of the soil.

Here we shall not discuss the physical, pedogenetical effect on the soil induced by the earthworms which has enormous implications with regard to soil permeability and structure with its applied correlates (drainage, yield of the soil, possibility of oversowing the grassland, (Bouché, in press), but shall focus on the eco-metabolic aspect of organication – mineralization cycles of biogenetic elements. We shall describe the data collected, preferably quantified *in situ*, and present a strategy to approach the problem.

2. Method to study the role of the earthworm within the mineralization-organication process

Besides numerous qualitative *in situ* studies, almost all our knowledge is established in experimental situations that are sometimes very artificial and sometimes apparently «close to nature» (to what we imagine nature to be like). The result of these quantified data is extrapolated to «field» situations without being able to assess whether they are valid or no there. Therefore suitable techniques should be devised to verify these extrapolations. Finally, one should distinguish data obtained *in situ* without knowledge of functional structures, either because they are unstable (frequent ploughing), or because the technique used does not take into account these time-space structures (e.g. supply input through isotope markers of global fertilizer without relation to these structures, without respecting the forms of the biogenetic element present in the soil at the concentration of these forms at a particular site, at a particular time; another example: misrepresentation of a block of soil by taking a horizon of soil without regard to the functional diversity of the *loci* that this block encloses).

These difficulties of concept and techniques may be partly solved (or even completely solved, would it not be for the scarcity of information) by giving clear priority to ecological data (Bouché, 1977), i.e. to data obtained in a situation of quasi non-perturbation (extremely well balanced environment as occurs in a real permanent meadow).

In this context, the anecic earthworms may constitute a real physio-pedological probe (Bouché, in press) by allowing the study of the exchange activities of the soil without disturbing its structure, and by respecting the coupling of the chemical (consumers of fertilizer) and physical (exergonic, reactions), including

biophysical (incorporation, pulverization, transposition...) and biochemical activities (decomposition, fixation, mineralization, reorganization).

It is, therefore, possible to use the physio-pedological probe formed by the anecic worms in three complementary ways starting from the soil surface:

1) by marking an accessible compartment, such as vegetable litter, by means of an isotope that will be followed into the soil up to the probe that acts as a receptor;

2) by marking the anecics that so play the role of emitters (sources) *in situ*, and following some elements in different receptor compartments;

3) by using the material that results from fungal and microbial digestive activity accessible at the surface, i.e. the fresh «turricules» that one can collect and analyze.

In theory it is possible in all these cases to use a natural or artificial marker.

These three approaches have been practiced *in situ*: the first by Dietz (1979), the second by Ferrière (1985), the third by Rafidison (1982). In spite of the scarcity of data and their heterogeneous character (Dietz = Mediterranean meadow vegetation on clay-mud soil + *Nicodrilus caliginosus meridionalis*; Ferrière = meadow in semicontinental climate with muddy soil + *Nicodrilus longus longus*; Rafidison = forest of *Fagus sylvatica* in semicontinental climate with sand-mud soil + *Nicodrilus velox*), such studies have yielded valuable information. The most recent information is that provided by Ferrière & Bouché, (1985); Bouché & Ferrière, (1986). Measurements were taken during spring plant growth, with limited litter, and sub-optimal activity conditions. This study allowed an effective measure, *in situ* of the nitrogen output and the results were in agreement with laboratory findings reported by Ferrière & Bouché (1985). Under these laboratory conditions Ferrière also measured transmetabolic carbon output (Bouché, 1984; Ferrière, 1985).

In the wake of studies by Rafidison (1982), Bouché (1983), using many chemical elements as markers, clarified the mechanisms of internal incubation, and improved the theoretical framework, mainly by demonstrating the reingestion of the faeces after they have undergone a maturation outside the intestine.

Only the qualitative data of this study will be used in the present paper.

Dietz (1979) performed pioneer study in which litter was marked and then traced in the soil. Unfortunately because of a lack of knowledge of the internal mechanisms of the soil, this study has been used very little and then only in purely qualitative terms (Dietz & Bottner, 1981). The interest of Dietz's data derives above all from the fact, that the transfers have lasted 68 weeks (they overlapped in spring) from February 15, 1978, to June 1st, 1979, during the period of plant growth: the first spring with measured litter and no labelled faeces; and the second spring with unmarked litter and labelled faeces. The

drawback of Dietz's data is their relative inaccuracy. The present article aims to reinterpret these data using recently demonstrated mechanisms: while Dietz has observed the movements *in situ* plants → earthworms, Ferrière has established the transfers earthworms → plants.

However, the cycle via dead roots as food source will not be discussed further in the present paper.

2.1 Mechanisms and theoretical scheme

In the absence of earthworms it seems that micro-organisms (and also a certain microfauna) are responsible for the essential part of the decomposition-mineralization; the diffusion of organic matter occurs mostly through gravity (particularly rain washin) we shall call this part of the cycle (transfer + transformation) of the elements, the PMP circuit (physico-chemical, microbial, plants). This is the classical circuit described in pedology, culture and microbiology manuals (Fig. 1).

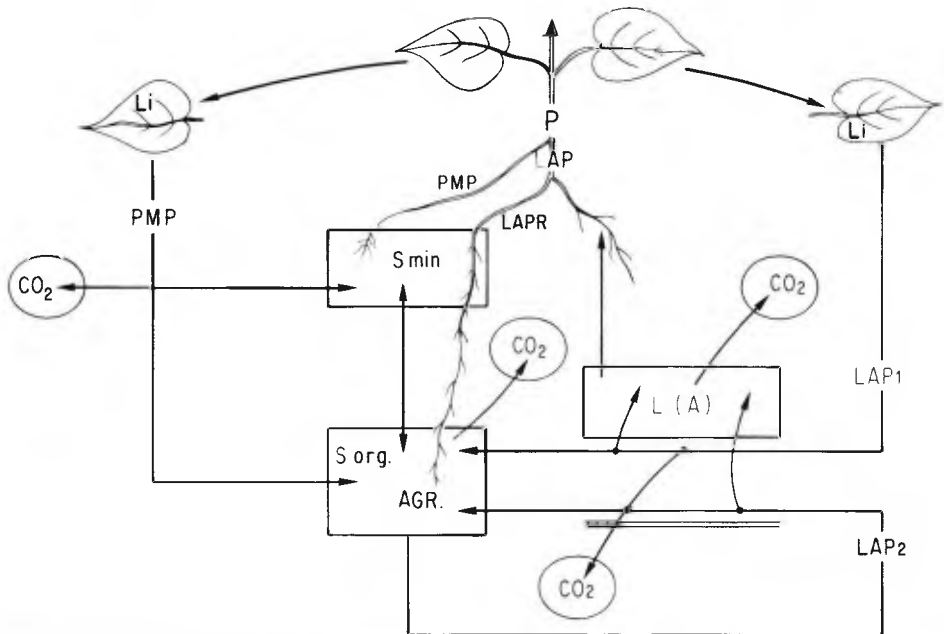


Fig. 1 – Circuit of the elements from plant to plant: 1) through a classical, purely physico-chemical process (PMP: on the left); 2) through a process from the litter to anecic towards the plants (LAP: on the right), either directly through the earthworm metabolism (LAP1), or after recycling (LAP2), or by root extrapolation of the faeces (LAPR). (S min = mineralized stock; S org = organic stock containing Agr; L(A) = anecic biomass; Li = litter; P = plants).

Moreover, in the presence of anecic earthworms, the litter is ingested on the surface, digested, partly assimilated, then rejected, after a transit in the earthworm metabolism, by discharge (excretion, respiration).

The elements that are not assimilated are deposited as faeces, particularly rich in litter debris (Dietz, 1977) and are reingested *after a post-anal incubation* (Bouché, 1981), that is after a delay of perhaps 6 or 7 weeks (the fresh faeces seem to be toxic (Kaplan et al., 1980)). These faeces represent more than 50% of the intake of *Nicodrilus velox* in spring (Bouché et al., 1983). Finally, part of the faeces is colonized by the roots (Bouché, in press) that exploit the aggregates in course of mineralization, and in the meanwhile, as we have shown (Bouché & Ferrière, 1986), the nitrogen eliminated by the earthworms passes rapidly and completely into the plants. The whole mechanism of decomposition of the litter through the anecic is obviously constantly related to a microbial activity which is very intense because the intestinal incubation enhances the vital microbial condition. We shall call this circuit LAP (litter → anecic → plants). The LAP circuit can be divided into three processes: – primary LAP, called LAP 1, where the movement of the elements follows the scheme Litter → ingestion → digestion → assimilation → earthworms → discharge → (if necessary a brief microbial mucolysis) → plant assimilation.

– secondary LAP, called LAP 2, where the elements pass via litter → ingestion → digestion → defecation → post anal incubation → reingestion → digestion → assimilation → earthworms → discharge → plants (the assimilation may occur after several digestions → defecations).

– root LAP, called LAPR, where the elements pass via litter → ingestion → digestion → defecation → post anal incubation → roots (there can be several digestions followed by defecations before the incubated faeces are exploited by the roots).

3. Balance of the transfer of carbon and of nitrogen in spring in permanent meadows, attempt of a synthesis

Sources:

1) Dietz (1979) for the carbon cycle *in situ* with earthworms and without earthworms, litter regression of *Lolium perenne*.

2) Ferrière (1985), for the nitrogen cycle *in situ* and the C/N ratio in the laboratory.

3.1 Rate of litter regression

Figure 2 shows the rate of disappearance of the litter from the soil surface (% of average ^{14}C activity); note the total disappearance between the 48th and 68th week.

Functions without earthworms: $y = e^{-0,0419x + 4,574}$
 $y'_0 =$ elimination output = 4,059% / week (percent of the activity of the initial ^{14}C of the litter), y'_0 is measured from the onset ($t = 0$) that is when the litter presents all its stable and unstable fractions on the soil.

Functions with earthworms: $y = e^{-0,016x + 1,607} + e^{-1,130x + 4,5871}$ $y'_0 = 12,8\%$ per week.

3.2 Speed of mineralization

Figure 3 gives the rate of mineralization of the buried or unburied litter (all the ^{14}C of the system) in the presence or absence of anecics.

Absence of earthworms:

$$y = e^{-0,02155x + 4,5822}$$

output: $y'_0 = 2,106\%$ per week

Presence of anecics:

$$y = e^{-0,00655x + 3,367} + e^{-0,116x + 4,2988}$$

output: $y'_0 = 8,73\%$ per week

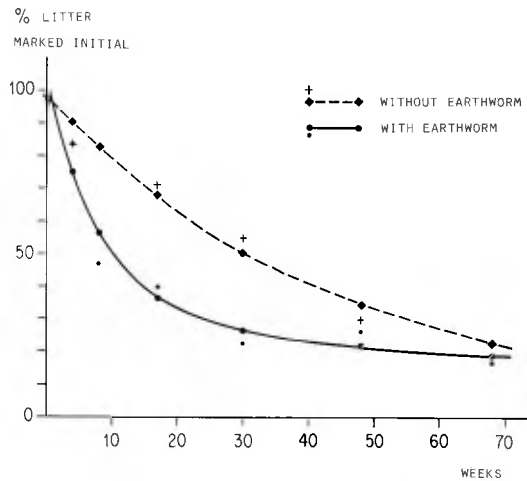


Fig. 2 – Disappearance (decomposition and burying) of the litter of *Lolium perenne* marked with ^{14}C (after Dietz, 1979) without earthworms (observed: crosses; adjusted: broken line) or in the presence of *Nicodirus caliginosus meridionalis* (observed: dash; adjusted: straight line).

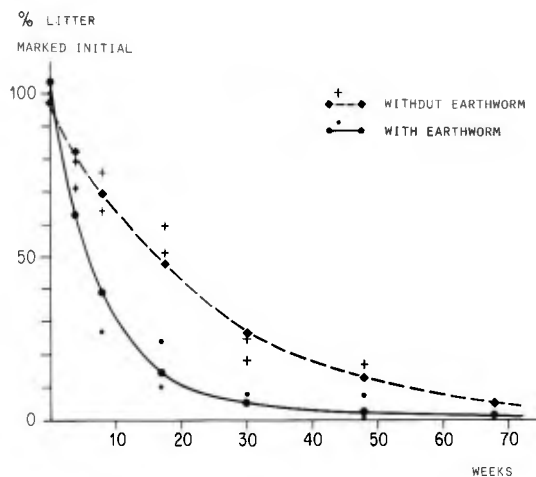


Fig. 3 – Rate of decomposition of the organic matter (in and on the soil) accumulated initially on the soil (litter of *Lolium perenne* and degraded in the absence (observed: crosses; adjusted: dashes) or presence of *Nicodrilus caliginosus meridionalis*. (observed: dash; adjusted: straight line).

3.3 Output in the earthworm

Under the experimental conditions described by Dietz (1979) the «endogeic» behaviour of *Nicodrilus meridionalis* allowed him to chose in the soil an environment close to optimum as «thermohygropreferendum» in subvertical burrows (Bouché, in press), that is close to 12°C for a *Nicodrilus* «anecic» near to *N. longus*. We know that between the soil and laboratory measurement, the Q_{10} may be about 2 (Bouché & Ferrière, 1986) and that the carbon output is 0.1376 mg C/g body weight of C/day at 15°C, that is to say 0.1118/day/12°C. Under these conditions, the 8 g hm (= humid matter) of earthworms used by Dietz (that is 600 mg body C) discharge each week through this metabolism $0.1118 \times 7 \times 0.6 = 0.469 \approx 470$ mg C/week. The C/N of established transbody output based on the results of Ferrière is 4.5 (Bouché, 1984) so that this metabolic nitrogen amounts to 105 mg N/week.

3.4 Budget of the transfert litter → soil (PMP + LAP) (Tab. I)

The monoliths and columns of Dietz have received 10 g dm (dry matter) of litter at 100% initial radioactivity with a rate C = 45% of dm (= 4500 mg) and a

TABLE I - Assessment of exchanges of elements (dm = dry matter; hm = humid matter, %/d = percentage of litter expressed in dry matter.

Emanation based on Ferrière (= F)

EMANATION C

Output Ferrière

= 0.1376 g/g C/day (15°C)

Output with $Q_{10} = 2$

= 0.1118 g/g c/day (12°C)

= 782.6 mg/g C/week (12°C)

For each monolith there are 8 g hm earthworms on 600 mg corporal C

$0.782 \times 0.6 = 0.469$ g/week

output per monolith = 470 mg/week

EMANATION N

470 mg C = C/N 4.5 = 105 mg N

Initial litter per monolith (Dietz = D)

1 monolith = 100% radioactivity = 10 g dm = (45%) = 4.5 g C = (C/N = 40) = 112,5 mg N

Assessment	with earthworms			without earthworms			LAP 1	
	%/s	mg C	mg N	%/s	mg C	mg N	mg C	mg N
In 1 hour								
Burying (D)	12.8	576	14.4	4.059	182.65	4.57	373.4	9.83
Output VdT (F)	-	470	105	-	0	0	470	105
Total mineralization (D)	8.72	392.4	9.81	2.106	94.77	2.37	297.6	7.44
Deposit (D)	3.63	161.1	4.03	1.953	87.88	2.20	75.8	2.39

C/N = 40 or 112 mg N. It is to be supposed that the releases of N and C are proportional to the mineralization.

3.5 Accumulation of marked carbon in *N. meridionalis*

The carbon stemming from the litter initially tends to accumulate (Fig. 4) as the only source during the first spring with the litter, while during the second spring, this litter drawing disappeared (Fig. 2) it is, on the contrary, a solely in soil source that furnishes the ^{14}C .

To our surprise during the adjustment by non linear regression by reiteration on computer, the function of accumulation took the form:

$$y = e^{-0.073x + 4.92} + e^{-0.075x + 4.92}$$

perfectly symmetrical between two functions, one of entry (\approx assimilation) the

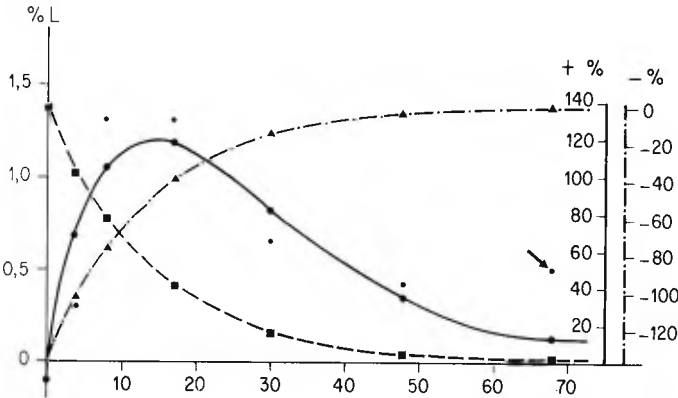


Fig. 4 – Adjustment of the accumulation of ^{14}C from a marked litter at the beginning of the experiment (= 100%) in the tissues of *N. caliginosus meridionalis* (% observed: dots; adjusted: large dots) and approximate kinetics of accumulation assimilation of ^{14}C (+ % triangles) compensated by an emanation (- % squares). Note the point of the 68th week (arrow), not taken into account, probably reflecting a resumption of the ^{14}C elements previously incorporated into the excrement-aggregation.

other of exit (\approx emanation), of the same volume $e^{4.92} = 137\%$ of volume) (too high the supply being 100%), and of emanation output = assimilation = 10% / week $\approx 450 \text{ mg C} / \text{week}$ ($\approx 11.25 \text{ mg/N/week}$), value really very close to the 470 mg C established in section 3.3. It seems that the entry or exit function is only a simple exponent, contrary to those related to the earthworms (this article and above all Ferrière & Bouché, 1985; Bouché & Ferrière, 1986), this with regard to the low number of points-used (6), which prevents an adjustment to 8 parameters, and requires a calculation based on 4 parameters. This unavoidable choice indicates a fault in the curving of the curves and perhaps the excess of the asymptotes «propped up» to 137%.

Likewise, we know that in spring and in soils the nitrogenous excrements of the earthworms are completely mineralized (Ferrière, 1985), this is probably also the case of the carbon related to these excrements. The carbon output of the circuit LAP 1 shown in Tab. I based on data by Ferrière (470 mg C/week) should therefore be mineralized where as the value observed by Dietz is lower (248 mg/week). The difference of 36% may seem important but it only underlines two phenomena:

1) the mineralization of the excrements takes some time (average time: 10 days, Fig. 5);

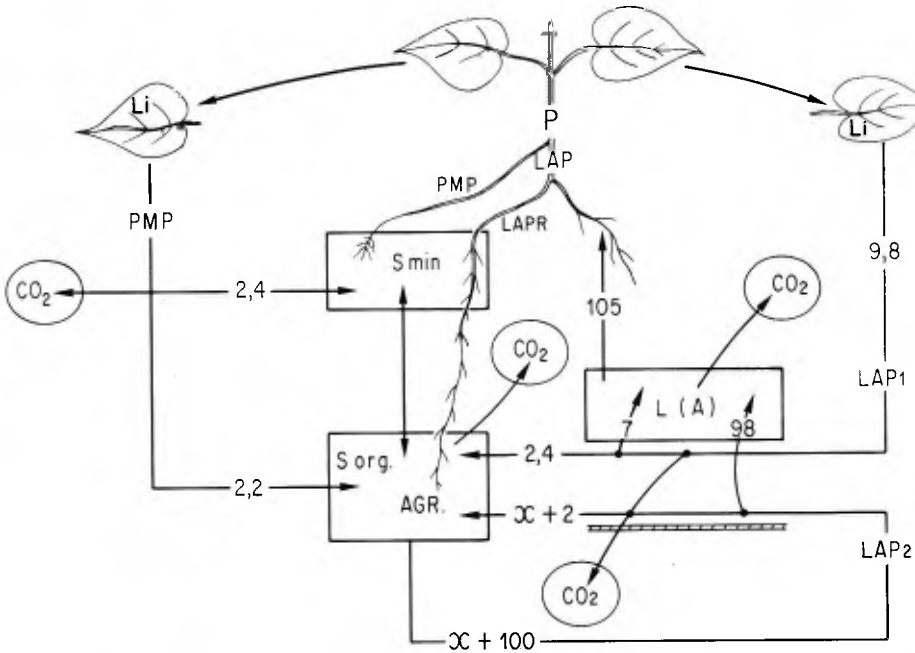


Fig. 5 – Approximate assessment of the nitrogen movements incorporated in the soil per 8 g hm of *Nicodrilus* in spring, through the PMP and LAP circuit (x indicates stemming quantities from organic stocks (S org.) and returning to the soil as aggregates via an intestinal transit (see legend to Fig. 1).

2) the calculation given in Tab. I implies that Dietz data are accurate and that the theoretic extrapolation (Q_{10}) are correct. Now we know that this can only be true to a certain extent. It is already remarkable that these calculations that compare two very different sources, converge with only such small difference.

One can therefore conclude that despite the weak information there is good agreement between the extrapolations from Ferrière (1985), and the adjustments from Dietz (1979): the orders of quantity calculated with the two methods make up with each other.

At the end of a year, the earthworms feed on litter practically unmarked since autumn (new plant production without ¹⁴C marking), the carbon on and in the soil is essentially of ¹²C. However, one year later, the earthworms contain in at near equilibrium of exchanges (assimilation = discharge) ca. 0.45% of the initial radioactivity, this value having to be compared with the maximum of the body marking of the previous year ca. 1.30%. Taking into account the radioactivity

apparently diluted in the soil, the supplies of initial ^{14}C are therefore not negligible one year after its incorporation into the soil. Here again we find further proof for the functioning of a LAP 2 circuit: a preferential ingestion of excrements where the ex-litter ^{14}C resides preferentially.

3.6 *Nitrogen requirement of the earthworms and supply*

We have seen that the metabolic output of nitrogen of earthworms (Fig. 5) is about 105 mg N/week (rough evaluation, source Ferrière). The supply from the fresh litter (LAP 1) is equal to 7.5 mg; 97.5 mg N/week are missing! These come from the nitrogen concentrated mainly through/and in the microbial elements of the reingested organic matter. They are concentrated in rich elements (C/N ca. 8), but diluted in a heterogeneous mixture (C/N ca. 20) (Bouché et al., 1983); it needs at least $98 \text{ mg N} \times 20 = 1980 \text{ mg}$ or about 2000 mg/C, or with a low rate for the aggregation of 10% = 20000 mg/week of soil, or 2.8 g a day of soil treated by the earthworm (their humid mass of treated soil per day is currently assumed to be = 8 g); it is therefore probable that the earthworms deal at the most 6 g/day (ca. 42 g/week) of soil having at least 2000 mg C of soil of which 1000 mg C are mineralized releasing (C/N = 10) about 100 mg N/week (Fig. 6).

3.7 *Transfer of nitrogen from the earthworm to plants*

At this point we know that the quasi-totality of the nitrogen metabolized by the earthworms is not excreted through the digestive tract (this would be at least 1.3% of the defecated nitrogen even 1.5% the excreted nitrogen!). This nitrogen is completely assimilated by the plants with remarkable effectiveness (more than 96%) according to simulated kinetics (Fig. 7) (Bouché et al., in preparation). There is a peak of nitrogen to be assimilated by the plants (ammonia, urea) followed probably by a delayed assimilation because of the mucolysis (proteolysis) of the mucus. This involves the LAP 1-2 circuits. The exploitation of the earthworm aggregations by the roots, which is very important (so much so that an aggregative function has been attributed to the roots) would therefore refer to a nitrogen of plant origin without metabolic transit in the earthworm, only transferred via the digestive tract. LAPR is from this point of view a circuit «without earthworm metabolism», but «under an earthworm digestive mechanism».

During the experiment conducted by Ferrière (1985) in spring, the incorporation of nitrogen into the plant of the grassland was measured ($272 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). The emanation of *Nicodrilus longus longus*, actually observed in this meadow

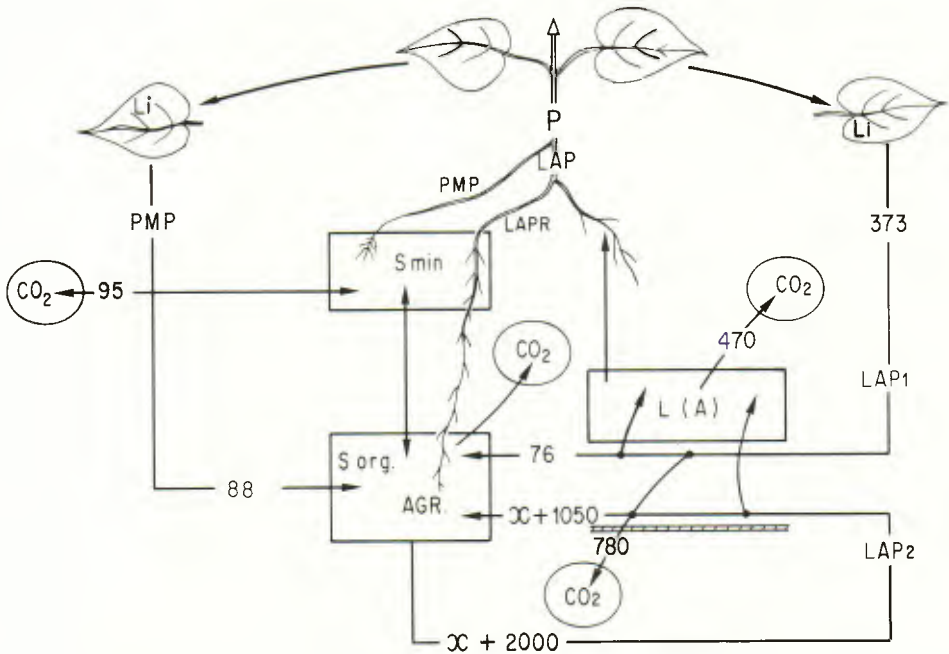


Fig. 6 – Approximate assessment of the carbon movements incorporated in the soil per 8 g hm of *Nicodrilus* in spring, through the PMP and LAP circuit (x indicates the quantities stemming from stocks (S org.) and returning to the soil as aggregates via an intestinal transit (see legend to Fig. 1).

only in the adult stage, accounts for 25.8% of this assimilation, extrapolating this quality on the totality of anecic, this account for 60% of the plant assimilation, and if the totality of earthworms discharge nitrogen in a comparable manner, 82% of the nitrogen assimilated by plants is supplied via the earthworms. This illustrates the importance of the LAP 1 - 2 circuits for plants in spring (Tab. II).

3.8 *Approximate assessment of the PMP + LAP movements in spring*

The LAP circuit compared with the classical eumicrobial circuit is very important with regard to the burying and the mineralization of organic matter. (Figs. 6 and 7). Consequently, the carbon deposit is proportionally lower (Tab. III).

The role of earthworms in the decomposition and nitrogen nutrition of plants in a grassland

TABLE II - Extrapolation of the nitrogen quantities released by the earthworms to the whole population of the Cîteaux (Ferrière, 1985).

SPECIES	Biomass from 13/4 to 22/5 g (mph)/m ²	Output (mg/day/m ²)	Satisfaction of the plant need per day (%)
<i>Nicodrilus longus</i>	47.82	70.3	25.8
<i>Nicodrilus nocturnus</i>	17.88	26.3	9.6
<i>Nicodrilus anecic</i> (young)	46.53	68.4	25.0
Total anecic	112.23	165.0	60.0
Epigeus			
<i>Lumbricus castaneus</i>	4.54	6.7	2.4
<i>Allolobophora icterica</i> (adult + young)	26.05	38.3	14.0
<i>Allolobophora rosea</i> (adult)	3.34	4.9	1.8
<i>Nicodrilus caliginosus</i> (adult)	1.11	1.6	0.6
<i>A. rosea</i> and <i>N. caliginosus</i> (young)	5.67	8.3	3.0
Total endogenous	36.17	53.2	19.4
Total earthworms	152.94	224.9	82.5

TABLE III - PMP + LAP circuit in spring.

	Burying	Mineralization	Endogeic deposit
PMP	1/3	1/4	55%
LAP	2/3	3/4	45%

The assessment of the LAP circuit is very important because its very rapid kinetics, this is the «short circuit of the ecosystem» where the plant nourishes the earthworm that nourished the plant rapidly (LAP1) or less rapidly (LAP2), more indirectly (LAP R). The LAP 2 circuit that «empties» in spring its store of post-anal rations, most probably replenish it in autumn, even in winter by making up a fixed nitrogen store through the reorganization of the latter trends to its close mixing with fresh organic matter (and therefore with energy) incorporated in the soil. To bury 13.8 mg, in the presence of earthworms, only 9.3 mg pass directly to the plants through LAP 1 (Tab. I) and about 95 mg come from the soil essentially through LAP 2.

This preliminary assessment from facts directly observed in grasslands represents only a very active spring period, its extrapolation to the whole year is at the

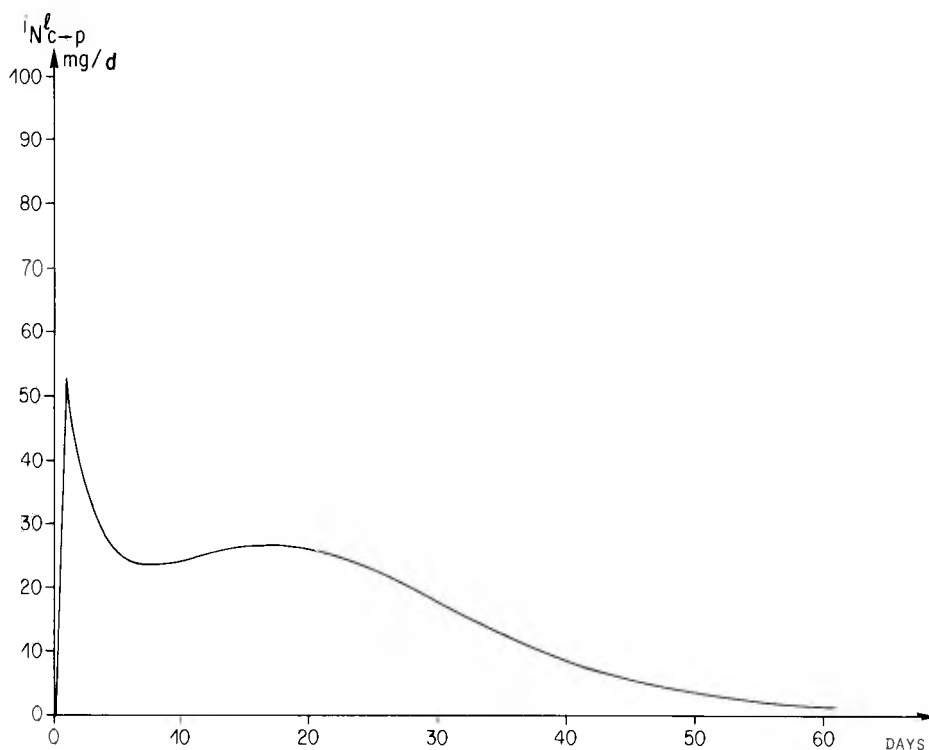


Fig. 7 - Absorption of initial nitrogen of earthworm origin by the plant after its emanation into the soil by the earthworms. Note the bimodal characters of the curve (after Ferrière, 1985).

moment only possible *on the lead of the earthworms section*, since we have an index of anecic activity together with a study of the environmental factors acting on this activity (Heidet & Boucbé, unpubl.). Unfortunately, we do not possess any information of the annual systems of litter production in grasslands.

4. Discussion and Conclusion

The experimental method employed to study ^{14}C from litter is more open to criticism than that of the measurement of the passage of nitrogen from the earthworms to the plants (LAP 1 + 2).

The two main reasons for this are: 1) the ^{14}C from litter is supplied

«roughly» (10 g for 314 cm² or 318 g/m² or 3.2 T/ha), which could correspond to an exceptional post-winter (effect of situation) although it probably corresponds to a post-summer or summer situation (aging of plants). A most more precise knowledge of the rate of formation of the litter should be taken into account in our experiments. 2) the composition of the marked litter is that of dead plants after marking and not that of real litter (the vegetable composition is modified by aging and falling to the ground through microorganisms). Concentration of biogenetic elements in the ex-living cells and microorganisms and the real C/N relationship of the accessible litter could differ from that of the introduced marked litter. In addition, herbivores, especially in intensified meadows, concentrate in distinctive patches: their faeces, even their urine, the elements of this source cannot be neglected in the humid period of the beginning of spring.

Throughout this text, the mechanisms described tend to ignore the intestinal excretion of nitrogen, potentially possible, for the earthworms. This probably occurs at the level of Morren's gland to increase the pH in acid soils with the help of ammonia (Bouché et al., 1983), but it would largely be reabsorbed, almost totally (about 1.3% of the excreted nitrogen is formed via the digestive tract, (Ferrière, 1985). Toutain (1981) actually observed a relative digestion of the intercellular locus very rich in nitrogen (brown bodies of leaves of beech = 65% of the total nitrogen of the litter), during the intestinal transit in *N. velox*; the nitrogen circuit oriented in the direction soil → earthworm is very intense in the digestive tract parallel with a correlated loss of carbon «at the digestive level» (pre-oral incubation of the litter, digestion, post-anal incubation...). The result shortly after transit (1 to 2 days) is the presence of biogenetic elements relatively mineralized in the faeces of earthworms and then quickly re-organized by post-anal incubation. More detailed studies of these mechanisms are called for. These are therefore good reasons to interpret the C losses (mainly release of CO₂, but also production of Ca CO₃ through the Morren's glands) as intervening at the «digestive» level *sensu lato*, from plant death on and up to the deposit of the faeces (1 or 2 days later depending on the methods used to collect the casts).

Considering the output of nitrogen through the adult *Nicodrilus longus longus* compartment measured at Cîteaux in spring, the size of this compartment (biomass) and the activity condition (Heidet & Bouché, unpubl.), allows us to try to extrapolate for the whole years the output of nitrogenous excrements of this stage and taxon in this grassland.

Unfortunately we do not have the measurements of the activity index of *N. longus* during the experiments of Ferrière (spring 1983), but only the thermic conditions at -10 cm (average 8°C) (the hydro-conditions (pF < 3) and the length of the day not being limiting factors).

A first calculation allowing a Q₁₀ = 2 and corresponding to a thermic

equivalent for an average annual activity index $Mib = 1$, actually observed in February (= 4.2° C) indicated for an average biomass of 47,82 g hmp·m⁻² a day output of 70 mg·d⁻¹m⁻², which give fixes for this stage an excretion of 197,2 Kg·ha⁻¹·y⁻¹ (Ferrière, 1985).

The study of Heidet & Bouché allows the weekly calculation of the activity in relation to the estimate biomass through washing/sieving (= bl_{60}): ($\sum Iab \times bl_{60}$) 52 weeks = 3700.6 that related to the output of 105 mg N/gN and per days observed *in situ* by Ferrière gives:

$$\text{Annual output} = \frac{105.033 \times 0.016 \times 7 \times 3700.63}{1.42} = \frac{30657 \text{ mg/m}^2}{306.6 \text{ kg/ha}}$$

(1.42 = Iab at 8°C with pF and length of day not limiting; 0.016 = body concentration of nitrogen in the humid earthworm mass).

However, during this experiment the earthworms have selected a hygrothermal preferendum, thanks to their vertical burrows (Bouché, 1987), that tends to be 12°C. Under these conditions, the coefficient Iab passes from 1.42 to 1.75 and the estimated annual output of excretion is only 248 kg/ha. Since there is nothing better we retain this fork to be of 250 ± 55 kg/ha of nitrogen excretion for 478.3 hg/hmp/ha of adult *N. longus*.

The extrapolation of this value to all the anecics of Cîteaux (1122 Kg/ha) and to the earthworms (1530 kg/ha) gives a total excretion of respectively 586.6 kg N/ha/year and 800 kg N/ha/year. These discharges are probably greater than the needs of the plants (which are indeed not well known) and would indicate a recycling in the microbial biomass.

In conclusion, the first incomplete assessments of the functioning of the grassland that we present, demonstrate:

1) that it is technically feasible to make these assessments during the year in the most fertile soils, i.e. those having a complete earthworm fauna with a prevalence of anecics;

2) the preliminary data obtained with two different approaches are in accordance;

3) the possibility to follow «instant» plant production during its post-mortem evolution would allow us to understand its role better, not only in its intrinsic chemical evolution (which is classical), but above all in its energetical and physical future (rhythm of formation-destruction of the aggregates, for example);

4) paradoxically, it is our lack of knowledge of the seasonal variations of the litter formation that may hinder these studies (but solutions are in view: Gounot, 1982).

REFERENCES

- Bouché M. B., 1981 – Contribution des lombriciens à la migration des éléments dans les sols en climats tempérés. C. R. Coll. int. CNRS «Migrations organo-minérales dans les sols tempérés». Nancy, 24-28 sept. 1979, n° 303, Ed. CNRS, 145-153.
- Bouché M. B., 1984 – Une méthode de mesure du débit d'éléments dans un sol non perturbé: azote et carbone des lombriciens (Lumbricidae: Annelida). *Pedobiologia*, 27, 197-206.
- Bouché M. B., 1987 c) – The subterranean behaviour of the earthworm. This volume, 159-169.
- Bouché M. B., in press a) – Prairies et vers de terre: un potentiel de progrès insoupçonné.
- Bouché M. B., in press b) – Une sonde pour l'étude fonctionnelle des échanges d'éléments en sol non perturbé.
- Bouché M. B., Ferrière G., 1986 – Cinétique de l'assimilation de l'azote d'origine lombricienne par une végétation prairiale non perturbée. C. R. Acad. Sci. Paris, 301, III, 17, 789-794.
- Bouché M. B., Z. Rafidison et F. Tourain, 1983 – Etude de l'alimentation et du brassage pédointestinal du lombricien *Nicodrilus velox* (Annelida, Lumbricidae) par l'analyse élémentaire. *Rev. écol. biol. sol*, 20, 1, 49-75.
- Dietz S., 1979 – Etude de l'incorporation de la litière en système herbacé à l'aide de matériel végétal marqué au ¹⁴C. Thèse 3ème cycle; Ecologie terrestre. USTL Montpellier, 12/11/79, 1-78.
- Dietz S., Bottner P., 1981 – Etude par autoradiographie de l'enfouissement d'une litière marquée au ¹⁴C en milieu herbacé. C. R. Coll. int. CNRS «Migrations organo-minérales dans les sols tempérés». Nancy, 24-28 sept. 1979, 303, Ed. CNRS, 125-143.
- Eckardt F. E., 1972 – Une grande entreprise s'achève: le programme biologique international. *Bull. soc. écol.*, 3, 369-375.
- Ferrière G., 1985 – Mouvements naturels des éléments dans une prairie: quantification des échanges d'azote entre lombriciens, sol et plantes. Thèse docteur d'Etat en sciences, Univ. Lyon I.
- Ferrière G., Bouché M. B., 1985 – Première mesure écophysiological d'un débit d'éléments dans un animal endogé: le débit d'azote de *Nicodrilus longus longus* (Ude) (Lumbricidae, Oligochaeta) dans la prairie de Citeaux. C. R. Acad. Sci. Paris.
- Gounot M., 1982 – Analyse et modélisation de l'écosystème prairial. *Acta Oecol., oec. gen.*, 3, 7-28.
- Kaplan D. L., Hartenstein R., Neuhauser E. F., 1980 – Coprophagic relations among the earthworm *Eisenia foetida*, *Eudrilus eugeniae* and *Amyntas* sp. *Pedobiologia*, 20, 74-84.
- Rafidison Z., 1982 – Rôle de la faune dans l'humification: transformation des feuilles de hêtre par un ver anécique (*Nicodrilus velox*). Thèse Doct. pédologie, Nancy I, 1-104.
- Satchell J. E., 1963 – Nitrogen turnover by a woodland population of *Lumbricus terrestris*. In «Progress in soil biology», F. Vieweg, Ed. Braunschweig, 102-109.
- Toutain F., 1981 – Les humus forestiers: structures et modes de fonctionnement. *Rev. forest. franç.*, XXXIII, 6, 449-479.

G. FERRIÈRE

Museum d'Histoire Naturelle, Mairie, F-21000
Dijon (France)

M. B. BOUCHÉ

Laboratoire de Zooécologie du sol, CEPE,
INRA/CNRS, BP 5051 F-34033 Montpellier
Cedex (France)

P. SOTO

Laboratoire de Zooécologie du sol, CEPE,
INRA/CNRS, BP 5051 F-34033 Montpellier
Cedex (France)